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NATIVE BUNCHGRASS AND INVASIVE WEED ESTABLISHMENT IN LOW
NUTRIENT RANGELAND SOILS WITH NITROGEN AND PHOSPHORUS
MANIPULATION

by

Jeffrey S. Burnham

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2010

ABSTRACT

Native Bunchgrass and Invasive Weed Establishment in Low Nutrient Rangeland Soils
with Nitrogen and Phosphorus Manipulation

by

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Utah State University, 2010

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Competition between native perennial grasses and *Bromus tectorum* has been studied for many years. Recently, soil nutrients have been immobilized in an effort to preferentially inhibit growth of *B. tectorum* relative to native species. Most of this work has focused on soil N, but interactions with soil P are less studied and may be important as well. Additionally, although competitive effects and nutrient responses of several *Centaurea* spp. are well documented, data are lacking on the competitive effects that *Centaurea virgata* exerts on the establishment of native and exotic communities. A field experiment and a greenhouse experiment were conducted to evaluate influence of N and P on the native perennial bunchgrass *Pseudoroegneria spicata* in competition with *B. tectorum* and *C. virgata*.

Chapter 2 describes the effects of nutrient immobilization and subsequent 2 x 2 factorial additions of N and P. Treatments were applied to transplanted individuals of the study species in monocultures and mixtures. Analysis of variance (ANOVA) was

performed on shoot dry mass, soil water content, and physiological responses including photosynthetic rate, stomatal conductance, and transpiration. Results suggest that *B. tectorum* may be P-limited in certain circumstances, and that physiological activity of all species is subject to interactions between available N and P.

In Chapter 3, I assess response of the study species to 2 x 2 factorial additions of N and P on a very low-nutrient soil in a greenhouse. Relative effects of different species mixtures on *P. spicata* are reported. I report ANOVA results of tiller number, leaf number, specific leaf area, shoot dry mass, root dry mass, and water addition. Results indicate that N and P co-limit *P. spicata* and *B. tectorum*, and to a lesser extent, *C. virgata*. *B. tectorum* showed the highest percentage response to fertilization. Land managers may be more successful establishing native grasses if they can minimize soil fertility.

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Jeffrey S. Burnham

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CHAPTER 1

INTRODUCTION TO RESEARCH ON NUTRIENTS AFFECTING THE INVASION OF SEMI-ARID STEPPE COMMUNITIES

INTRODUCTION

A substantial body of research has developed on the role essential soil nutrients play in regulating and facilitating plant growth and plant-plant interactions, be it at the individual, population, or community level. Some aspects of this role can be generalized, while others appear to vary based on individual circumstances, results of mechanisms we do not yet fully grasp. Much of this research is physiological in nature, but range scientists have tended to focus on population-level responses such as biomass, density, and cover. In recent years, they have begun to apply an understanding of nutrient limitation and its effect on plant succession to the problem of invasive weed control. Invasive species cause problems in most areas of the world, and the Intermountain West is no exception. It is hoped that the research herein will increase our ability in some small measure to successfully manage semi-arid rangelands in favor of more productive and more economical native perennial vegetation. A review of pertinent literature follows, sketching the context of plant succession and major characteristics of native grasses in general, and bluebunch wheatgrass (*Pseudoroegneria spicata*) in particular. Also reviewed are the behaviors of two important invasive weeds of the Great Basin, cheatgrass (*Bromus tectorum*) and squarrose knapweed (*Centaurea virgata*). After outlining nitrogen (N) and phosphorus (P) effects on plant growth, I present the main objectives of this thesis.

SUCCESSION AND NATIVE GRASSES

Competition for resources is important in structuring plant communities (Grime 1979, Tilman 1990), and N is the primary limiting nutrient in semi-arid systems (McLendon and Redente 1991, Tilman and Wedin 1991, Paschke et al. 2000). In drought conditions, N was more limiting even than water in one *Pseudoroegneria/Festuca* community (Blicker et al. 2002). Late successional species are traditionally thought to compete better than early successional species (Tilman 1982, 1988).

State and transition models hold that multiple sets of vegetative conditions can persist on rangelands, separated by potentially brief and unstable transition periods (Westoby et al. 1989, Tausch et al. 1993). *Bromus tectorum* invasion of the Intermountain West is such a transition that is triggered by disturbance, and *B. tectorum* dominance can be very stable indeed due to its competitive ability (Young and Evans 1985, Pyke and Borman 1993) and strong association with a drastically decreased fire return interval (Billings 1990). Melgoza et al. (1990) explain how certain life history traits of *B. tectorum*, including early germination and emergence, rapid root development, and early maturation and seed shatter while perennials are becoming water-stressed, allow it to persist once established. Though perennials can reinvade, competition from *B. tectorum* generally prevents this (Monsen 1994), and successful establishment of natives might well depend on reducing their exposure to competition early on. The native state of many western rangelands consists of shrubs and bunchgrasses with substantial bare ground (West 1988), and is considered a stable state (Laycock 1991) because grasses like mature *P. spicata* can exclude *B. tectorum* (Booth et al. 2003). Unfortunately, rapid restoration of invaded rangelands is unlikely to succeed (Monsen and McArthur 1995)

due to weed propagule pressure, relatively short-lived effects of herbicide, and competitive ability. Assisted succession (Cox and Anderson 2004) and seeding of cover crops in advance of native perennials has shown some promise, but ultimate restoration will likely require knowledge of fundamental ecological processes (Sheley and Krueger-Mangold 2003).

Pickett et al. (1987) identified three general causes of succession: site availability, species availability, and species performance, the last of which includes things like life history and ecophysiological traits. If we concentrate on the outcome of competition between natives and invasives when site characteristics change, then species performance will determine how succession proceeds. When displacing native species, invasive species can alter ecosystem processes, degrade wildlife habitat, decrease productivity, and end up costing \$2 billion annually (DiTomaso 2000, Evans et al. 2001). Invasion is most likely when disturbance combines with fertility increases (Burke and Grime 1996). Most invasives have high relative growth rates, and they also have a larger relative response to high fertility than slow growers (Lambers et al. 1998). One reason may be that unlike these high growth rate species, slow-growing plants are not capable of responding quickly to N (Chapin 1993) and are thus overtaken. More recently, the fluctuating resource hypothesis has stated that invasibility increases with increasing unused resources and increasing fluctuations of those resources (Davis et al. 2000). Disturbance is a pivotal event in such a context, because it is often associated with sudden pulses of nutrient availability in an otherwise low-nutrient system (Stubbs and Pyke 2001, Vazquez et al. 2008a), theoretically opening a space for invasion. Levels of N increase after fire and mowing and remain elevated for up to a year, presumably due in

part to increased net mineralization (Stubbs and Pyke 2005). Reduced plant uptake also contributes (Young et al. 1995), and it is mostly the elevated nitrate level, rather than ammonium, that tends to favor annuals (Paschke et al. 2000, Monaco et al. 2003).

Invasion often follows changes in soil processes (Ehrenfield and Scott 2001). Since fast-growing plants create feedback mechanisms and can grow exponentially (Radosевич et al. 2007, Vazquez et al. 2008a), swift action might prevent a colonizing population from initiating a difficult-to-reverse transition to a degraded state. But even in sites dominated by invasive species, identifying those process changes is the first step toward mitigation of negative impacts and ultimately restoration.

If Burke and Grime (1996) are correct, then invasion should be less likely when fertility is low, and this actually has been observed repeatedly (Huenneke et al. 1990, Kreuger-Mangold et al. 2006). McLendon and Redente (1991, 1992) found the rate and direction of secondary succession (succession following disturbance) from early to late semi-arid seral communities to be directly related to the lack of N availability, and competitive relationships change with changing N levels (Tilman and Wedin 1991). On the Colorado Front Range foothills, Paschke et al. (2000) reduced soil fertility with sucrose in a *B. tectorum*-dominated community, and in four years observed its conversion to a perennial-dominated community.

Late seral perennial plants are slow growing but competitive (Harpole 2006, Herron et al. 2001), and they persist at lower nutrient levels than invasives and should be able to outcompete them (Wedin and Tilman 1990). Indeed, the plant that can survive at the lowest level of the most limiting nutrient should thrive and outcompete all others (Tilman 1988). This prediction was borne out by a study in which Tilman and Wedin

(1991) observed late seral plants displacing early seral species in pairwise trials.

Several factors contribute to this pattern. Late seral plants have high root mass ratios, high nutrient resorption efficiency, and low rates of ion uptake, growth, and tissue turnover (Aerts 1999). Craine et al. (2002) outlined two strategies for maintaining plant biomass in low-nutrient soils: first, accession of a unique source of some nutrient; and second, production of low-nutrient biomass, including low physiological activity. Understanding nutrient assimilation rates and growth rates might facilitate predictions of plant dominance under given conditions (Pickett et al. 1987), and with enough discrepancy in these traits between annuals and perennials, it should be possible to predict community succession based on resource supply to plants (Krueger-Mangold et al. 2006).

A common method of exploring resource supply is the manipulation of soil nutrient levels through immobilization and fertilization. Immobilization is the process of making soil nutrients unavailable to plants, and is the opposite of mineralization. It is discussed in detail in another section below. Fertilization, while expected to favor early seral species, is used because a response to fertilization in a given soil implies nutrient limitation in that soil (Suding et al. 2004, Meiman et al. 2006). As will be shown, *B. tectorum* in particular is frequently limited by soil nutrients. For example, Dakheel et al. (1993) found that in competition with *Taeniatherum asperum*, another invasive annual grass, *B. tectorum* was strongly limited by N and P, and concluded that coexistence of the two species was more likely at low nutrient levels. This is the assumption about *B. tectorum* and native grasses such as *P. spicata* as well, but real questions remain about whether the magnitude of any limitation is large enough to actually favor native

perennials in a wide variety of settings. Weigelt et al. (2005) state that grass species with high growth rates can take up more mineral N than slow growers, and if this is true at all nutrient levels by a sufficient margin, succession might not proceed. Interestingly, the addition of a deficient soil nutrient can be associated with decreased tissue concentrations of that nutrient, because additions stimulate growth that can then exceed uptake ability (Daoust and Childers 2004) and result in more efficient nutrient use by the plant (Link et al. 1995).

Restoration is important for ecological, aesthetic, and economical reasons, and native restoration species have value that exotics do not (Roundy et al. 1997). One native species, *P. spicata*, can dominate semi-arid grasslands in North America. Many extant stands of *P. spicata* in the Intermountain West thrive in relatively higher-altitude sites, perhaps because of elevated precipitation (Blank et al. 2007). In areas with *Artemisia tridentata vaseyana*, *P. spicata* may even return in abundance to areas that have experienced post-fire *B. tectorum* invasion (Rosentreter and Kelsey 1991). Although *Elymus multisetus* and *E. elymoides* have some characteristics that make it competitive with *B. tectorum* such as early germination and high growth rate (Luster 2002, Jones 1998), it is the *Festuca idahoensis*/*P. spicata* association that tends to be the most resistant to annual grass invasion (Blank et al. 2007). Despite this, and its presence in numerous restoration seed mixes, *P. spicata* has vulnerabilities and can be sensitive to competition from *B. tectorum*. Many natives are competitive when established, but their establishment is difficult because of competition (Velagala 1997). Reduced native establishment can prevent long-term native recovery (Brooks and Pyke 2001). The exact nature of this competition remains a research problem, because less has been learned

about the mechanisms of successful establishment than the factors governing interactions between adult plants (Sakai et al. 2001). Particular interspecific relationships are detailed in the next two sections, but besides behaving as the slow-growing late seral grass it is as described above, *P. spicata* is often affected less by intraspecific competition than is *B. tectorum*. Several researchers have found that interspecific competition of *Centaurea maculosa* inhibits growth of *P. spicata* more than does intraspecific competition (Jacobs and Sheley 1999, Seastedt and Suding 2007). *Bromus tectorum*, on the other hand, is more affected by intraspecific competition than by some perennial grasses, including *Bouteloua gracilis* (Lowe et al. 2002).

Competitive outcomes between *P. spicata* and *C. virgata* could be difficult to predict: besides the life form differences, important differences may exist between *C. virgata* and other more-studied knapweed species. As herbaceous monocots invest more in roots and less in leaves than herbaceous dicots (Garnier 1991), competition for nutrients might be anything from especially influential to not at all. If results in other semi-arid systems are any indication, the answer could have managerial implications.

BROMUS TECTORUM

B. tectorum is a winter annual grass native to Eurasia (Mack 1981), and usually cleistogamous. Invasive annual grass dominance is one of North America's most destructive plant invasions (Vazquez et al. 2008a). Annual grasses dominate 3.3 million acres of the Intermountain West, and 76.1 million more are susceptible (Pellant and Hall 1994). According to D'Antonio and Vitousek (1992), annual grasses like *B. tectorum* and *T. asperum* (Dakheel et al. 1993) threaten productivity by changing fire regimes,

nutrient cycling, and competitive relationships. These grasses are typified by early germination, rapid growth, and fine fuel production, leading to fires that have caused substantial changes in ecosystem processes (Pyke 2003). Knapp (1996) estimated that \$20 million is spent fighting *B. tectorum*-fueled fires, and Chambers et al. (2007) reported that the fire return interval in these areas has declined from 30-110 yrs to 3-5 yrs, which is insufficient for native survival (Whisenant 1990).

Bromus tectorum is also associated with soil nutrient changes, including N and P (Booth et al. 2003, Evans et al. 2001). Following invasion, soils can experience reduced N availability due to increased uptake. This condition can be exacerbated when any N-containing litter leachate is then immediately reincorporated into new biomass, and the removal of N-fixing soil crust depletes N levels even further (Sperry et al. 2006). Rimer and Evans (2006) observed a 50% decrease in the labile N pool subsequent to invasion by *B. tectorum* and attributed it to changes in litter quality. While evidence is strong that *B. tectorum* affects N availability, this might be a function of biomass incorporation and increased volatilization rather than novel chemistry. Bolton et al. (1990) found lower net N mineralization rates under *B. tectorum* than native grasses, but Svejcar and Sheley (2001) did not, and they also failed to observe altered soil N mineralization, total C or N, or total standing biomass in one site invaded by *B. tectorum*. And in another study on the Colorado Plateau, *B. tectorum* had higher litter mass C:N ratios than natives, and litter production altered nutrient cycling (Evans et al. 2001). Nor do interactions with soil biota appear to result in decisive changes to the soil. *B. tectorum* can access native grass mycorrhizal networks (Belnap and Sherrod 2009) and may quickly acquire mycorrhizae in desert soils (Allen 1984). Despite these benefits, however, *B. tectorum* does not

appear to influence the soil biota, including the AMF community, in ways that increased its success (Rowe and Brown 2008).

Another trait of *B. tectorum* is plasticity, which tends to result in seed production every year and allows the species to behave as a K-strategist. Depending on drought tolerance and resource availability, seed production can be highly variable and voluminous (MacArthur 1962, Mack and Pyke 1983). In addition to morphological plasticity, *B. tectorum* enjoys the ability to germinate in spring or in fall, and fall root growth increases its spring competitive ability (Dobrowolski et al. 1990). Specifically, *B. tectorum* transpiration in spring depletes soil moisture for other seedlings (Monson 1994). High relative growth rates following disturbance allow many invasives to establish more quickly and survive later stress (Grotkopp and Rejmanek 2007). These traits fit several of those mentioned by Baker (1965) as characteristic of the “ideal weed:” high seed output and a rapid transition from a vegetative to a reproductive state.

Specific leaf area is strongly associated with relative growth rate (Leishman et al. 2007), although it might not always be advantageous (Hamilton et al. 2005), and it can be reduced by low nutrient availability (Taub 2002). Consistent with the efficiency generally typical of perennial grasses compared to annuals, *B. tectorum* has much more leaf area than *F. idahoensis*, but equivalent specific leaf area (Goodwin et al. 1999). It should be noted that equivalent specific leaf area does not imply equivalent growth rate.

Few invasive rangeland species receive as much attention in the literature as *B. tectorum*, but its physiological activity is less-studied. For example, although it begins drawing soil moisture early in the season compared to most perennials, it is apparently unclear whether perennials are also impacted by concurrent transpiration and stomatal

conductance in maturing *B. tectorum*, or if the cumulative season-long desiccation of the soil is the main inhibitor.

Herbicides such as glyphosate and sulfometuron methyl offer significant, if sometimes short-term, control of *B. tectorum*-dominated sites, but propagule pressure and seed banks often lead to the return of *B. tectorum* in the absence of continuing application and/or aggressive reseeding and other management interventions (Pellant et al. 1999). The plant's plasticity, competitiveness, and ability to alter fire regimes and even soil properties have thwarted efforts at restoration and have made it difficult to control. In fact, Belnap and Sherrod (2009) report that competition from *B. tectorum* often impedes native seedlings.

Yet there are indications that restoration of native perennials might be feasible on the basis of resource supply. If establishing native seedlings in *B. tectorum* monocultures has met with only marginal success, adults on the other hand can compete successfully. Blank et al. (2007) note that in general, *Festuca/Pseudoroegneria* associations are more resistant to *B. tectorum* invasion than *E. elymoides/Poa secunda/Stipa comata* associations, and *E. elymoides* and *E. multisetus* themselves can inhibit *B. tectorum* to some extent under certain nutrient availability levels (Luster 2002). Cox and Anderson (2004) reported increased native success in Utah's West Desert when they were planted into stands of *B. tectorum* that had first been seeded with *Agropyron cristatum*, a perennial introduced grass. Similarly, initially seeding a disturbed area (a recently burned *B. tectorum* stand, for example) with a cover crop such as annual rye has also resulted in a *B. tectorum* reduction (Vazquez et al. 2008b). This phenomenon appears to be caused in part by the annual rye filling a niche, and appropriating an excess nutrient—

probably N (see below). Nitrogen plays an important role governing relative success of vegetation, and this fact has been exploited. For instance, on a granitic soil, *Bromus mollis*, another annual brome, outgrew the perennial *E. glaucus* at high but not at low N (Claassen and Marler 1998). More relevant to the Great Basin, McLendon and Redente (1991, 1992) found that secondary succession on a semi-arid site in Colorado could be managed in favor of annuals or perennials based on the amount of available N, with increasing fertility favoring annuals. Nearly three decades have passed since these landmark studies, and on the whole, underlying competitive mechanisms between *B. tectorum* and *P. spicata* are still not well understood (Vazquez et al. 2008b). This should be corrected, because prospects of managing successful native-dominated communities hinge on a thorough understanding of fundamental ecological relationships between the natives and the invasive weeds (Krueger-Mangold et al. 2006).

CENTAUREA VIRGATA

Centaurea virgata is reported throughout the western states, and while it is not nearly as dominant as other knapweed species such as *Centaurea maculosa* and *Centaurea diffusa*, a particularly large infestation of 150,000 acres exists in Utah, well south of the largest populations of those congeners (Roche and Roche 1991). It is a true perennial forb with a deep taproot, and occasionally persists as a basal rosette for multiple growing seasons. The extent to which these rosettes accumulate resources for subsequent bolting and the strength of any association between rosette size and future fecundity as seen in some short-lived perennial forbs (Lacey 1986), is unknown. According to an unpublished progress report of an interagency demonstration plot in Juab

County, Utah (Scott Jensen, *personal communication* 2001), *C. virgata* has a number of traits that happen to be typical of weedy species: although first year shoot growth is generally restricted to rosettes, it can resprout after fire and flower in the same year; it can germinate and produce seed within one year in the absence of dense intraspecific competition, although seed formation generally occurs in July and August; seed is highly viable; effective herbicides also remove most other dicot vegetation as well; and the recurved burs on its seed heads make it prone to spread via wool, hair (Roche et al. 1992), and other means.

Concerns about *C. virgata* stem from its tendency to form dense monospecific stands in parts of west-central Utah, and from fears that it could invade much larger areas like its close relatives *C. maculosa*, *C. diffusa*, and *C. repens*. Taken together, these three species have infested millions of acres across the North American prairies and the Intermountain West, especially the northern tier (Roche and Roche 1991, Skinner et al. 2000, LeJeune and Seastedt 2001). They are highly destructive (Lacey et al. 1989, Sheley et al. 1998). Resource supply offers some hope for managing the control of these species, because soil nutrients tend to limit knapweed species more often than they do *P. spicata*, which has a different interaction with the soil community than the knapweeds do (Meiman et al. 2006). This differential limitation is more apparent on low-nutrient sites, where *P. spicata* is often more competitive than knapweeds (Prather and Callihan 1991, Velagala 1997). There are situations in which *C. diffusa* can outcompete *P. spicata* for P, however (Callaway and Ashehoug 2000). These knapweeds can possess annual, facultative biennial, or perennial growth habits. Allelopathy has been documented from *C. maculosa* populations (Callaway and Ashehoug 2000, Ridenour and Callaway 2001),

although additional observations are inconsistent with that account (Suding et al. 2004). It is true that *C. virgata* shares several characteristics with these problematic species, but caution should be taken in assuming too many similarities. Although they did not examine *C. virgata*, Muth et al. (2006) were unable to identify clear phenotypic differences among invasive and non-invasive members of *Centaurea*, and concluded that even where they might exist, they probably are not solely related to fitness, but to various interactions. *C. virgata* has occurred in the Great Basin for over fifty years and has not yet expanded like other knapweeds. Nevertheless, it does enlarge its range when uncontrolled.

C. maculosa responds positively to N addition (Story et al. 1989), and the genus in general benefits from high resource conditions (LeJeune and Seastedt 2001). Although *C. maculosa* outcompeted *P. spicata* for N in one experiment, *P. spicata* has greater N use efficiency (Blicker et al. 2002). Despite this advantage, *P. spicata* did not have an earlier effect on *C. maculosa* biomass (Lindquist et al. 1996). This is consistent with findings that attribute considerable competitive ability to established *C. diffusa* (LeJeune et al. 2006), which apparently needs to be released from competition to successfully invade. Once established, however, it persists. Suding et al. (2004) found that *C. diffusa* was more tolerant of neighboring plants than *A. desertorum* and *B. japonicus*. Others found that reducing N and P did not produce the opposite effect of adding it (LeJeune et al. 2006). In other words, these knapweeds respond positively to N addition but do not experience reciprocal reductions in biomass when soil nutrient levels are impoverished. Knowledge of the extent to which *C. virgata* might share this capability would be useful.

This competitive trait highlights the importance of effecting expeditious native grass establishment in disturbed areas prone to knapweed invasion.

The early stages of knapweed invasions are not well studied, but *C. diffusa* appears to exploit high nutrient availability and especially the absence of grass competition to invade (Seastedt and Suding 2007). Rigorous investigation of *C. virgata* invasions in particular is almost wholly lacking, with much more attention having been devoted to the other members of *Centaurea*. Since Blicher et al. (2002) already found that competition and soil effects are not responsible for all of *Centaurea*'s expansion, quantitative evidence of precise limits placed upon *C. virgata* by biological and nutrient factors is needed.

EFFECTS OF NITROGEN

Nitrogen dynamics are closely associated with the tendency of many ecosystems to be invaded (Chapin et al. 1996), and invasive species are often favored by high soil N (Goldberg 1990, Burke and Grime 1996), so recent research has attempted to facilitate restoration by lowering soil N content. Nitrogen is generally less abundant in more arid soils (Chambers et al. 2007), so reducing it below native levels can have dramatically limiting effects on production. Nevertheless, late seral species were better able than early seral species to absorb N when it was low in a shortgrass-steppe system (Redente et al. 1992). Scarce N is usually made scarcer with a soil amendment of labile C such as sucrose or finely ground sawdust (Jackson et al. 1989, Svejcar 2003, Zink and Allen 1998), although more dramatic methods such as topsoil removal have been tried in a European grassland (Kardol et al. 2008). However, topsoil removal is not practical on a

rangeland scale. Soil C stimulates microbial growth, which takes up (immobilizes) N in the process of incorporating C, making the N unavailable to plants (Vitousek 1982, McLendon and Redente 1992), although the effect can be relatively ephemeral (Reever Morghan and Seastedt 1999). For C addition to reduce abundance of weeds that outcompete natives at high resource levels, the weeds must be more nitrophilic than natives and the N reduction must endure long enough to make a difference (Blumenthal 2003), which at least sometimes happens (Tisdale 1985).

However, the strategy has produced mixed results. McLendon and Redente (1992) observed more species, perennial forbs, and perennial grasses—an absolute increase in desirable species—in sucrose treatments than non-sucrose treatments on a semi-arid Colorado site. On a tallgrass prairie site, C addition greatly increased native biomass growth, and while changes in competition could have been the case, soil water availability or increased light penetration also might have been factors (Blumenthal et al. 2003). Sucrose and nitrapyrin (which prevents nitrification) decreased annual density and increased perennial density, especially density of *A. hymenoides*, whereas N addition increased growth of annuals (Young et al. 1995). Compared to high N conditions, invasive root mass had a greater % reduction at low N than did perennial root mass, including *P. spicata* (Monaco et al. 2003). Encouragingly, *P. spicata* can be relatively unaffected by soil amendment (Seastedt and Suding 2007). More often, however, annuals and perennials are both affected, with annuals showing the most sensitivity (Redente et al. 1992, Morgan 1994, Young et al. 1997, Paschke et al. 2000).

Unfortunately, reducing N availability does not always alter the competitive relationship between plants. Annuals can still outperform perennials at low N availability

(Young and Mangold 2008), and James (2008a) and Berendse et al. (1992) also saw similar responses to N in fast- and slow-growing grass relative growth rates. Looking at *B. tectorum*, *B. gracilis*, *C. maculosa*, and *Pascopyrum smithii* (a native perennial rhizomatous grass), Lowe et al. (2002) found no general response to N; that is, no root-shoot ratio, biomass, or leaf tissue N differences among species or groups, but only within species. *B. tectorum*, for instance, competes well at low levels of N (Young and Mangold 2008), and even when early seral species compete poorly for N, they compensate with high rates of growth and reproduction (Tilman and Wedin 1991). For instance, Craine et al. (2002) found that non-leguminous plants with high biomass produced low-N tissue rather than acquire more N. Vazquez et al. (2008b) observed a greater growth rate in *B. tectorum* at any level of N tested, including that of unamended river-washed sand, than in perennial grasses, leading them to suggest that N is not the sole driver of invasion. James (2008b) agrees that reducing soil N levels alone will not favor perennial grasses over annual grasses. And Blicher et al. (2002) inferred phenotypic plasticity in the short-lived perennial forb *C. maculosa*. They observed it rapidly take up N when colonizing disturbed areas absent much competition, and yet it still competed for nutrients with grasses once established, which subsequently has been observed on a *P. spicata*/*F. idahoensis* site (Mangold and Sheley 2008). This came as a surprise, since N deprivation should inhibit growth in a species that requires N to maintain biomass. Rarely, N fertilization even appears to increase late seral performance (Krueger-Mangold et al. 2004).

But if perennial grasses are not favored at low N, it could be sufficient for purposes of establishing a population that they are not inhibited, at least not by other

species. Despite failing to observe a relative increase in perennial vegetation at low N, Lowe et al. (2002) did note a reduction in competitive interference. Using finely ground straw as a C source mixed into soil, Monaco et al. (2003) observed that in response to nutrient immobilization, all species of seedlings, including *B. tectorum*, *T. asperum*, and *P. spicata* suffered equal amounts of reduced growth. This led them to speculate that with low enough N, annuals and perennials may be similar enough to allow for native establishment and recommended experiments quantifying the resource demands of particular species groups in response to N.

Several factors, including sucrose application rate, could account for part of the variation in results. In one study, sucrose did not lead to a relative increase in *P. spicata* compared to *C. maculosa*, leading Mangold and Sheley (2008) to speculate that an insufficient amount of N was immobilized. Blumenthal et al. (2003) suggest that the amount of organic matter/m² needed to observe significant native facilitation, approximately 7250 g, is much greater than the amount needed for weed suppression (1000-1500 g). These numbers are more applicable to mesic areas; Mazzola et al. (2008) used 150 g, a rate common to the lower-nutrient environment of the Great Basin, and observed a 67% decrease in *B. tectorum* biomass. Alternatively, the particular species involved could explain differences. In one *A. tridentata*/*E. elymoides* system, the ability of perennials to sequester soil N over a longer time frame than *B. tectorum* probably helped these species to compete for low soil N (Booth et al. 2003). Species growing actively for a greater portion of the year should be more capable of compensating for low N than ruderal species that mature and reproduce rapidly, whereas competing populations with strongly overlapping growing seasons might exhibit a more similar response to

nutrient changes. Biological responses can vary so widely that “perennial grasses” might not correctly be thought of as a functional group when it comes to the effect of N mineralization and nitrification (Wedin and Tilman 1990). It is also possible that these explanations are interacting with changing nutrient levels. Fire suppression, grazing, and atmospheric deposition have increased soil N availability in many areas (Fenn et al. 1998), but in some semi-arid areas, N levels have actually decreased (Evans and Ehleringer 1994). Furthermore, invasives can decrease N through repeated fires and volatilization (Mack and D’Antonio 1998, Blank et al. 1994). Most other nutrients are derived from the soil, but N comes from the atmosphere, is highly mobile, and is rapidly lost back to the atmosphere (Peterjohn and Schlesinger 1990, Fenn 1998). Finally, soil biota could be affecting successional outcomes more directly than through the immobilization of nutrients. Studying a South African grassland, Craine et al. (2007) describe the microbial N mining hypothesis as the increased decomposition of recalcitrant organic matter by some microbes using labile C as a way to obtain N, and it means that litter decomposition would increase when N is low. Arbuscular-mycorrhizal fungi effects are not clear. C addition resulted in lower infection rates, but the reduced shoot mass associated with low-N environments was supported by a proportionately large root and hyphal system (Jonasson et al. 1996).

This kind of site and species specificity makes it potentially difficult to precisely predict the effects of C amendment on succession. In any case it appears that low N could be an effective tool for restoration, but availability must be kept continually low and competition-tolerant seedlings of desirable species could also be required (Masters and Sheley 2001, Mazzola et al. 2008). In summary, the practicality of C addition

depends on site fertility, particular species involved, type of C, and interaction with other management techniques (Blumenthal et al. 2003). Exploiting this technique, then, demands considerable knowledge of each candidate restoration site.

EFFECTS OF PHOSPHORUS

Phosphorus is another soil macronutrient required for plant growth. It has been the subject of somewhat less attention to restoration ecologists than N, perhaps because of the complexity of its soil chemistry (McBride 1994). However, it can alter successional processes (Vitousek and White 1981) and the lack of it has limited plant production in a variety of situations. Although McLendon and Redente (1991) did not observe an effect of P in a semi-arid system, Sharpley (2000) suggests that total values of P between 100-3000 mg/kg soil make it a potentially limiting nutrient in many systems including grasslands, and N and P consistently co-limited production in a South African grassland (Craine et al. 2008). In this experiment, P added alone produced no biomass response, but N and P together produced a greater response than N alone (Craine et al. 2008). Redente et al. (1992) observed that N and P co-limited perennial and annual grasses in a shortgrass-steppe system. Krueger-Mangold et al. (2004) agree that P is a possible limiting nutrient in the warmer, drier areas of western Montana, where *C. maculosa* and *C. diffusa* are widespread. This, perhaps, led LeJeune and Seastedt (2001) to speculate that *Centaurea* spp. may be highly successful due in part to high competitiveness at low P levels. Others have also documented a change in the competitive response of these knapweeds in response to P changes (Lindquist et al. 1996). They also attributed reduced plant biomass following soil nutrient

impoverishment in this system to absolute decreases of N and P, rather than only a modified N:P ratio. In fact James (2008a) cautions against inferring too much from a particular N:P value, although N:P ratios themselves can be accurate predictors of nutrient limitation (Craine et al. 2008).

Phosphorus limitation is not thought to be restricted to more xeric sites, however. Atmospheric deposition and agricultural input have increased N levels on prairies such that LeJeune and Seastedt (2001) proposed that many native prairie and grassland species in North America are no longer N-limited, and could be P-limited. This led them to suggest successful restoration of grasslands will require the reestablishment of N limitation. But immobilization of N is not logistically trivial, so if ambient N levels are rising, it is possible that some manner of P immobilization could offer an alternative tool for restoration.

For Jonasson et al. (1996), C addition immobilized both N and P, suggesting the shortage was likely consequential in reducing growth. P limitation could account for some of the growth reduction observed in immobilization studies, although it is not always controlled for. In other cases, P reduction following sucrose application has not been detected (Mazzola et al. 2008, Seastedt and Suding 2007). In fact, Seastedt and Suding (2007) were unable to immobilize P in a Colorado Front Range grassland even after applying gypsum, and they concluded that *C. diffusa* is neither P limited nor especially competitive for N, which was the most likely driver of competition effects in their experiment. It is probable that they did not use enough gypsum, because gypsum can be very effective in binding phosphate (Brauer et al. 2005). Expense and unforeseen interactions could of course preclude large-scale gypsum application. An earlier study

found that both absolute soil P levels and N:P ratios appeared to affect *C. diffusa* (Suding et al. 2004), and lower P levels eliminated its competitive advantage over various native species. While this release of neighbors from competition is consistent with several studies on low N, its contradictory outcome relative to Seastedt and Suding (2007) suggests a complete understanding of relevant mechanisms, and of how to tie up P, still escapes us. Furthermore, it is not at all clear whether LeJeune and Seastedt (2001) were right and that P effects are behind the success of other members of *Centaurea*, like *C. virgata*. Others (Belnap et al. 2003) have used calcium oxide and ferric oxide to bind soil P, strongly decreasing emergence of *B. tectorum* and suggesting a restoration strategy in the process. If treatments could be applied that successively encouraged *B. tectorum* germination (like NO_3^-) and discouraged emergence (like CaO or Fe_2O_3) the result would be reduced competition and gradual depletion of *B. tectorum* in the seed bank. Even without considering emergence and germination, *B. tectorum* growth is nutrient-limited in winter (Miller et al. 2006), probably by Mn and/or P (Belnap and Sherrod 2009); the latter found that winter growth is actually correlated with available P. If *B. tectorum* winter growth could be significantly curtailed by restricting its access to P, then that aspect of its life history that confers such a competitive advantage in acquiring early season soil moisture (see above) could be partially mitigated.

Smith (1992) noted that P might constrain the rate of N fixation and ultimate availability, and N has been found to accumulate more rapidly in high-P soils (Schlesinger 1991). Microbial P peaked in summer and winter rather than fall and spring in a New Zealand hill country soil (Perrott et al. 1992). If this seasonal pattern holds for semi-arid cold desert environments like the Great Basin, most plant growth would then be

out of phase with maximum P availability, because other soil nutrients tend to be most available in spring and early summer (Blank et al. 2007). Phosphorus could feasibly limit growth even in soils that might otherwise not suggest the possibility. Regardless of seasonal bioavailability, much adsorption and precipitation of P occurs in calcareous soils (Caldwell et al. 1991), and P is most often constrained in such soils by carbonates and free calcium (Barber 1995). These soils are typical of many areas in the Great Basin, and P in fact can be low here (Lentz and Simonson 1987). *Pseudoroegneria spicata* is known to compete for it (Caldwell et al. 1987), but its influence on shoot mass is in some doubt. In one study, intraspecific size differences in *P. spicata* shoot biomass were unrelated to its ability to obtain P (Caldwell et al. 1991), which suggests that comparing root-shoot ratios in *P. spicata* at different P levels would help resolve the extent to which P affects below-ground structures.

Although weeds have been shown to generally increase with increasing nutrient availability, there is some evidence that their performance can vary. In one study including annual kochia, weeds minimally responsive to P became less competitive as P application increased (Blackshaw and Brandt 2009). If this result is analogous to annual grasses outcompeting native perennials on fertilized sites, then it is most likely due to relatively increased growth of other species more responsive to P. Nutrient form, or perhaps salt stress, could have played a role in the decreased growth of *B. tectorum* and not *Hilaria jamesii* in monocultures receiving sodium and potassium phosphates (Belnap and Sherrod 2009). Notably, when *B. tectorum* was grown next to the native grass, its biomass increased substantially compared to itself in monoculture. There is precedent for this sort of native facilitation of weedy species: Herron et al. (2001) and Callaway and

Pugmire (2007) both reported increased biomass of *C. maculosa* when growing next to native perennial grasses. This response also evokes the resource island theory, which suggests that soils underneath shrubs and trees will have higher nutrient levels (Stubbs and Pyke 2005) than nearby areas of bare ground. No woody vegetation exists in this case, but the natives are apparently acting as resource islands of some type. As in the case of N, the incidence of species-specific responses to changing P availability in a given soil implies that more species-specific experiments will be required before reliable generalizations are possible.

RESEARCH OBJECTIVES

The following chapters describe experiments that test the effects of different soil treatments designed to alter nutrient availability. Care has been taken to include P in this analysis, since the major part of previous research has focused on the role of nitrogen. The effects were measured through the responses of three species described in detail above, in competition with each other: the important native perennial bunchgrass *P. spicata*, the ubiquitous annual invasive grass *B. tectorum*, and the invasive perennial forb *C. virgata*, about whose competitive behavior relatively little is known. The overarching hypothesis is that low nutrient availability will increase the competitive ability of *P. spicata* against these weeds. On the relatively brief time frame of a single growing season, naturally nutrient-poor soil should have a similar effect to nutrient immobilization, so both conditions will be examined. These species co-occur or could potentially co-occur in many areas of the Great Basin, and knowledge of their interaction

under specific sets of conditions should enhance efforts to preserve existing native communities and to restore damaged ones.

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CHAPTER 2

EFFECT OF SOIL NITROGEN AND PHOSPHORUS MANIPULATION ON
BLUEBUNCH WHEATGRASS AND TWO RANGELAND WEEDS
IN THE GREAT BASIN

Abstract. *Bromus tectorum* causes widespread damage in the Great Basin of North America. Other exotic species also occur in the same region, often with smaller ranges and possible interactive effects with *B. tectorum*. *Centaurea virgata* is one such perennial species that has invaded semi-arid areas of Utah. We transplanted these species and the native perennial bunchgrass *Pseudoroegneria spicata* into a field site at the Tintic Valley Research Area, Juab County, Utah, into monocultures, all possible two-species mixtures, and the three-species mixture. After applying sucrose to immobilize soil nutrients, two levels each of nitrogen and phosphorus were factorially applied to all species treatments in an attempt to discover if either nutrient were limiting. Nitrogen addition increased dry shoot biomass of *P. spicata* and *C. virgata*, and P addition increased biomass of *B. tectorum*. Physiological traits were also measured, and three-factor interactions occurred on each species with varying results. Following presumed microbial nutrient uptake due to C addition, N and P can both limit production and physical traits of semi-arid vegetation. Research that identifies plant materials and strategies that maximize competitiveness of native vegetation over invasive species at low levels of both nutrients is needed.

INTRODUCTION

Bromus tectorum (cheatgrass) has invaded millions of acres in the North American Intermountain West (D'Antonio and Vitousek 1992, Pellant and Hall 1994), causing substantial economic losses (DiTomaso 2000). Fire return intervals have decreased drastically on invaded rangelands (Chambers et al. 2007), which has altered ecosystem processes (Pyke et al. 2003) and cost millions of dollars in fire suppression (Knapp 1996). *Bromus tectorum* is associated with changes in soil N and P availability (Evans et al. 2001, Booth et al. 2003). Since plant communities are strongly influenced by nutrient bioavailability (Goldberg 1990, Tilman 1990), these two important nutrients could be the basis of a mechanism responsible for some of *B. tectorum*'s remarkable success. Soil changes often occur in association with plant invasions (Ehrenfeld and Scott 2001), but it is not clear if soil condition is a causal agent or merely a consequence. Following one *B. tectorum* invasion on the Colorado Plateau, a 50% decrease in the labile N pool was observed (Rimer and Evans 2004), and in another, altered nutrient cycling was attributed to the large amount of litter produced with high C:N ratios (Evans et al. 2001). On the other hand, elevated N availability is widely recognized to follow disturbance such as fire (Stubbs and Pyke 2005, Vazquez et al. 2008a), and invasion is most likely when disturbance coincides with fertility increases (Burke and Grime 1996). Indeed, according to the fluctuating resource hypothesis (Davis et al. 2000), invasibility in general and invasion of *B. tectorum* in particular (Chambers et al. 2007) increases with resource availability, especially if resource dynamics are highly variable. Once established, *B. tectorum* germinates earlier, matures earlier, and disperses seed before native perennials, and the annual's large root system extracts enough soil water to stress

these perennials (Melgoza et al. 1990). *Bromus tectorum* is highly competitive (Young and Evans 1985, Pyke and Borman 1993) and can exclude native seedlings (Velagala 1997, Brooks and Pyke 2001, Mazzola et al. 2008). Effective *B. tectorum* suppression and/or native perennial facilitation on damaged wildlands would be an ecological and economic boon.

Centaurea virgata (squarrose knapweed) is much less widespread than *B. tectorum*, but has nevertheless gained a foothold of over 150,000 acres in central Utah and occurs throughout the Intermountain West (Roche and Roche 1991). *Centaurea* species—especially *C. diffusa*, *C. maculosa*, and *C. repens*—have invaded vast areas of North American prairies (Skinner et al. 2000, LeJeune and Seastedt 2001) with highly detrimental effects (Lacey et al. 1989, Sheley et al. 1998). Allelopathy has been proposed as a mechanism of invasion of *C. maculosa* (Callaway and Aschehoug 2000, Ridenour and Callaway 2001), although Suding et al. (2004) failed to confirm this. Alternatively, LeJeune and Seastedt (2001) suggested that *Centaurea* spp. have exploited a superior competitive response to nutrients, especially P, to invade. *Centaurea diffusa* in particular appears to benefit from the absence of grass competition in the establishment phase (Seastedt and Suding 2007). *Centaurea virgata*, unlike these other knapweeds, is a true perennial forb. It has a deep taproot, and can resprout after fire and form dense monospecific stands (Scott Jensen, *public communications* 2001). Capitula have multiple recurved burs, enabling it to spread via wool and hair (Roche et al. 1992). Little is known about its competitive interactions with other species or its response to nutrient availability, and while it has demonstrated invasive potential and shares many

characteristics with other *Centaurea* spp., enough differences exist to suggest that predictions that are not experimentally based will be unreliable.

Pseudoroegneria spicata (bluebunch wheatgrass) in association with *Festuca idahoensis* (Idaho fescue) is one of the plant communities most resistant to *B. tectorum* invasion (Blank et al. 2007), and *P. spicata* can even invade burned areas that have been colonized by *B. tectorum* (Rosentreter and Kelsey 1991). Thus, while *P. spicata* has potential as a restoration species and is common in reseeding mixes, little is known about competitive interactions in the establishment phase compared to relationships between adult individuals (Sakai et al. 2001). In fact, competitive mechanisms between *B. tectorum* and *P. spicata* are still not well understood (Vazquez et al. 2008b). Furthermore, the early stages of knapweed invasions have not been well studied (Seastedt and Suding 2007), and we are unaware of any published data on competition between *P. spicata* and *C. virgata* as seedlings or adults in any stage of invasion.

Resource competition strongly influences plant community structure (Grime 1979, Tilman 1990). Nitrogen is the principle limiting nutrient in many semi-arid systems (McLendon and Redente 1991, Tilman and Wedin 1991, Paschke et al. 2000), and may be even more important than water (Krueger-Mangold et al. 2004). By definition, late successional species tend to compete better for these resources (Tilman 1988, Harpole 2006). Compared to typical late successional species, many invasive species have high growth rates and a larger percentage response to increases in soil fertility (Lambers 1998). Many have observed that invasion is less likely under low fertility (Huenneke et al. 1990, Krueger-Mangold et al. 2006), and N availability can alter competitive relationships and control the rate of secondary succession (Tilman and

Wedin 1991, McLendon and Redente 1992). Fertility effects on plant community dynamics are often tested with soil nutrient immobilization and fertilization. Soil N availability generally decreases with aridity (Chambers et al. 2007), and can be reduced further with a soil amendment of labile C such as sucrose or finely ground sawdust (Jackson et al. 1989, Svejcar 1993, Zink and Allen 1998). Soil microbial populations immobilize N in the process of incorporating the C flush (Vitousek 1982, McLendon and Redente 1992), although the effect can be short-lived (Reever Morghan and Seastedt 1999). As a weed suppression strategy, this method requires weeds that are more nitrophilic than the desired vegetation (Blumenthal 2003). A positive vegetation response to fertilization implies limitation (Suding et al. 2004, Meiman et al. 2006), and suggests that immobilization would inhibit growth. If it inhibits early successional species more than late successional species, restoration becomes possible if immobilization can be practically achieved. Paschke et al. (2000) confirmed this possibility by converting a *B. tectorum*-dominated community to a perennial-dominated community in four years by reducing soil fertility. By better persisting at the lowest level of the most limiting nutrient (usually N), late successional species should be able to outcompete and ultimately displace most invasive species (Tilman 1988, Wedin and Tilman 1990). This usually occurs via either a unique source of a limiting nutrient or low physiological activity and the production of low-nutrient biomass (Craine et al. 2002). Thus, knowledge of nutrient assimilation and growth rates might lead to more accurate predictions of plant dominance under a specific set of conditions (Pickett et al. 1987). With enough discrepancy between invasives and natives, community succession based on plant resource supply should be predictable (Krueger-Mangold et al. 2006).

Like N, P is necessary for plant growth and can alter successional processes (Vitousek and White 1981). P and N have co-limited plant production in a variety of semi-arid systems, including a South African grassland (Craine et al. 2002) and a Colorado shortgrass steppe (Redente et al. 1992). Phosphorus could limit vegetation in the drier areas of western Montana (Krueger-Mangold et al. 2004), and some areas could be P-limited simply because increasing atmospheric and agricultural N input has rendered that nutrient less limiting (LeJeune and Seastedt 2001). Lindquist et al. (1996), however, found that decreasing knapweed competitiveness under low P was more likely a result of absolute reduction in P rather than a change in the N:P ratio. Species-specific responses are likely. Some annual weeds normally unresponsive to P actually became less competitive as P availability increased (Blackshaw and Brandt 2009). *Bromus tectorum* also appears to be P-limited, generally in winter (Miller et al. 2006, Belnap and Sherrod 2009). Phosphorus can constrain plant growth by controlling the rate of N fixation (Smith 1992). Interactions are to be expected, especially in high-P soils, which tend to accumulate N more rapidly than low-P soils (Schlesinger 1991). Phosphorus itself is influenced by soil type, and the carbonates and free calcium common in the calcareous soils of the Great Basin adsorb and precipitate substantial amounts of P (Caldwell et al. 1991, Barber 1995), causing low levels in some locations (Lentz and Simonson 1987). Finally, native species abundance could affect nutrient limitation of weeds. *Bromus tectorum* experienced increased production under low nutrients when grown adjacent to *Hilaria jamesii*, a native perennial grass, and a similar effect was observed with the invasive *C. maculosa* growing next to perennial grasses (Herron et al. 2001, Callaway et al. 2007). Soil variability is perhaps one reason for the inconsistent results in P

immobilization work. Soil P immobilization following C amendment has been observed by some (Jonasson et al. 1996, Redente et al. 1992) but not others (McLendon and Redente 1991, Mazzola et al. 2007), and Seastedt and Suding (2007) were unable to immobilize P even with gypsum. This suggests significant gaps in our understanding of soil P chemistry, and the possibility exists that previous immobilization studies might have overlooked P effects caused by soil amendments.

Because *C. virgata* could alter the dynamic between *P. spicata* and *B. tectorum*, we designed a transplantation experiment that would place establishing individuals of these species in competition during the growing season, when nutrients are most available (Blank et al. 2007). Our goals were to 1) evaluate the effects of per plant intra- and interspecific competition on established individuals of these species; and 2) simultaneously compare the results of soil nutrient immobilization with those of fertilization to assess the potential of N and P to co-limit growth in a field setting. We expected all species to respond with more growth at high nutrient levels, but that *P. spicata* would respond the least. We also predicted that *P. spicata* would be inhibited more by interspecific competition than intraspecific competition.

METHODS

Site Selection

Plants were transplanted into the Tintic Valley Research Area in Juab County, Utah (12S 401653 E 4411548 N NAD83), where cattle grazing has been excluded for over 50 years. Typical native vegetation includes *Juniperus osteosperma* (Utah juniper), *Artemisia tridentata wyomingensis* (Wyoming big sagebrush), *P. spicata*, *Elymus*

elymoides (squirreltail), *Pascopyrum smithii* (western wheatgrass), and *Calochortus nuttallii* (sego lily). *Bromus. tectorum* occurs, but generally not in large stands.

Centaurea virgata is common to abundant. Annual precipitation averages 30-36 cm and the elevation is approximately 1700 m. Soils are deep, well-drained mixed mesic Torrifluventic Haploxerolls (Luster 2002), and are mapped as part of the Juab loam series, 4-8% slopes. The ecological site is classified as upland loam, mountain big sagebrush (R028AY310UT).

Greenhouse Preparation

Soil was obtained from Skull Valley, Tooele County, Utah, then sieved. This soil is mapped as the Medburn series fine sandy loam, 2-8% slopes, well drained, with mean annual precipitation of 20-30 cm (Trickler 2001). Field soil was preferred to start the seedlings, and this one was chosen for its seasonal accessibility, relatively coarse texture (and thus ease of handling), lack of organic material and soil nutrient availability, and sparse plant cover in an area comparable to the field site in climate and potential vegetation community. On 19 Feb 2004, 450 cone-tainers were filled with soil and planted with three *P. spicata* seeds per cone and irrigated to saturation. Seeds were purchased from Granite Seed Company, Lehi, Utah. The procedure was repeated with *C. virgata* the following day, with seeds that had been personally harvested from near the field site at 12S 402673 E 4417704 N NAD 83. On 12 Mar 2004 the procedure was again repeated with *B. tectorum* seeds that had been personally harvested from near Vernon, Tooele County, Utah, approximately 12T 385121 E 4441041 N NAD83, then fully after-ripened. These two collection locations are in fairly close proximity and have

similar climatic conditions and potential vegetation. All plants received daily irrigation and were thinned as necessary to achieve a density of one individual per cone-tainer.

Transplanting and Treatment Application

Using the cone-tainers with plants described above, six replicates of seven different species treatments were implemented in the field, including all three monocultures, all possible two-species mixtures, and the three-species mixture. Each treatment consisted of six individuals arrayed randomly within a constant pattern within a 15-cm diameter circle, itself centered within a 1 m² treatment plot. Individuals were approximately equidistant from each other. In multi-species mixtures, conspecific individuals alternated with other species. Two-species mixtures had three individuals per species per plot, while the three-species mixture had two individuals per species per plot. Winter snowpack did not fully retreat from the field site until 22 Mar 2004, and transplanting occurred 31 Mar. The day prior, the field site was tilled to eliminate uncontrolled competition from unseeded *B. tectorum*, lightly compacted with a roller to control erosion, and surrounded with aluminum flashing to exclude Mormon crickets, which were observed in the area that season. The entire site was weeded throughout the season. After holes had been dibbled into the plots, they were filled with water, into which the seedlings just removed from the cone-tainers were placed. After transplanting was complete, all plots were irrigated with 1 cm of water. Identical irrigation occurred three, six, ten, and 13 days following transplanting. Like Lowe et al. (2002), we provided ample water to the plants because we wanted to test the effects of N and P, not water.

1500 kg/ha of sucrose was applied to the entire plot on 13 April 2004 to immobilize soil N and P (Wilson and Geary 1995, Jonasson et al. 1996, Luster 2002). Soaking rains wet the soil to several inches below the surface on 17 April, seventeen days after transplanting.

Nitrogen and P nutrient addition treatments were factorially applied to each mixture on 20 April 2004 for a total of four nutrient combinations. N-only addition consisted of 39 g/m² N (as 111 g/m² ammonium nitrate). P-only addition consisted of 64 g/m² P (as 147 g/m² triple super phosphate); others have used super phosphate (Seastedt and Suding 2007). N + P addition combined the previous two treatments. The final treatment, referred to as the control, received C addition like all others but did not receive any N or P. Nitrogen was applied at a slightly lower rate than P to maximize the possibility of a P effect and to reduce the likelihood of significant soil acidification by the ammonium nitrate. Nutrient treatments were supplied by commercial fertilizers, and after application, the study plots were irrigated with 1 cm of water a final time. Like some others (Blumenthal et al. 2003) the study location was hand weeded, mainly for *B. tectorum* that had emerged from the seedbank within some of the plots. Subsequent minor weeding occurred at intervals until approximately late May 2004.

Data Collection and Statistical Analyses

Soil gravimetric water content and plant physiological traits including photosynthetic rate, stomatal conductance, and transpiration rate were measured with a LiCor® 6400 gas exchange analyzer affixed with a red and blue light source and a 15-cm clamp on 21 May and 25 June, although the May data were compromised by an

equipment malfunction. Shoot biomass of all individuals was harvested in late July 2004, dried for 48 hr at 40 degrees centigrade in USU drying ovens, weighed, and stored. Nutrient immobilization in response to C was assumed, but direct soil nutrient analysis was not performed. Kardol et al. (2008) also inferred microbial N immobilization in response to C addition without direct measurement in a mid-successional *Agrostis capillaries*/*Festuca ovina* association.

There were 6 replicates of each combination of species mixture and nutrient treatment, treated as a randomized factorial design. Some dependent variables were natural log transformed to normalize the data distribution, and means and standard errors (SE's) presented herein have been back transformed for ease of viewing. Separate 3-way mixed model analyses of variance tested the strength of N, P, and species treatment on the responses of each species, with block as the random factor. Significance was set at $P=0.05$. Least squares mean separations were achieved with Tukey multiple comparison tests, $P=0.05$. All analyses were performed with SAS JMP 7 (SAS 2007).

RESULTS

Biomass

Table 2.1 and Figs. 2.1 and 2.2 show that N addition led to similar significant increases in *P. spicata* (24%) and *C. virgata* (29%) shoot dry mass relative to unfertilized plots. *Bromus tectorum* shoot dry mass did not respond to N but did respond directly to P addition (21% increase). Shoot dry mass of *P. spicata*, however, decreased with P by 15%. Mixture did not significantly affect performance of any species, nor did any interaction. Although it appears from Fig. 2.2 that *P. spicata* growth tended to respond

less to high-N conditions when in monoculture than in species mixtures, the variability was considerable and the N*Mix interaction was not significant. No obvious trends appear in *B. tectorum* and *C. virgata*, although the values for *C. virgata* biomass equal or exceed those of *B. tectorum*. In a similar trial in greenhouse conditions (see chapter three), *C. virgata* mean shoot mass did not exceed that of *B. tectorum*, particularly in the N + P fertilized treatment. Unsurprisingly for a late seral grass, *P. spicata* produced the smallest amount of biomass of the three species.

Physiology

Pseudoroegneria spicata (Table 2.2, Fig. 2.3) experienced a significant N*P*Mix interaction on photosynthetic rate, but no other factors were significant. This interaction was mainly driven by an unusual result in the *P. spicata* monoculture where control plants photosynthesized much more rapidly than N-treated plants (627%, Fig. 2.3). In contrast, control plants in monoculture were not only significantly more active than control plants in competition with *B. tectorum* (183%), but N-addition plants in the same mixture also outperformed them, although this latter result was not statistically significant. Additionally, the N + P plants in the three-species mixture also had significantly less activity than the monoculture control plants. In fact, means for N + P treatments were lower than N-only treatments for all mixtures except the monoculture.

No main effects or interactions were significant for *B. tectorum* photosynthetic rate. However, plants in the N + P treatment (Fig. 2.3) did have lower (nonsignificant) photosynthetic rates than did plants in all treatments except the three-species mixture (Table 2.2). *Centaurea virgata* (Table 2.2) was significantly affected by an interaction

between N and mixture, which could be partially explained by a 679% rate increase from low N to high N in the three-species mixture without a comparable increase in the other species treatments (Fig. 2.3).

Stomatal conductance (Table 2.3) in *P. spicata* was not affected by nutrient treatment or mixture, and no trends are obvious in Fig. 2.4. Conductance in *B. tectorum* (Fig. 2.4) was highest in control plants in the two-species mixture with *P. spicata*. In contrast, in the three-species mixture *B. tectorum* control plants had the lowest overall mean conductance (700% difference) for the species. The only species mixture in which *B. tectorum* conductance differed among treatments was the two-species mixture with *P. spicata*, which appears to be responsible for the significant three-way interaction in Table 2.3. As in *P. spicata*, *C. virgata* (Fig. 2.4) mean conductance was not significantly affected by any main effect or interaction (Table 2.3).

Effects on transpiration (Table 2.4) were similar to those found with stomatal conductance; there were no significant effects with *P. spicata* or *C. virgata*, but for *B. tectorum* the main effect of mixture and the N*Mix and N*P*Mix interactions were significant. The three-way interaction appears to have been driven by the two-species mixture with *P. spicata* and the three species mixture. In the former, transpiration was significantly greater in the N+P treatment and control treatment, while N-containing treatments in the latter both exceeded the control. The other two species treatments had no significant differences between nutrient treatments. The lowest overall value of *B. tectorum* transpiration occurred in the control treatment within the three-species mixture, which was also the case with conductance. Although they are not statistically significant, *P. spicata* results in Fig. 2.5 look similar to those in Fig. 2.4, with N-only-treated plots

tending to be lower than plots receiving only P, particularly in both two-species combinations with the invasives.

Soil Water

No significant main effects or interactions were observed in soil gravimetric water content in either May or June (Table 2.5). Mean values were typical of seasonal values (Nowak et al. 2006) obtained from nearby sites and vegetation communities, and ranged from 30%-39% in May and 22%-29% in June (Fig. 2.6). In June, a marginal N*P*Mix interaction might have been developing ($P=0.08$). The nearest Remote Automated Weather Station (RAWS), Mud Springs, is located approximately 12 km southwest of the field site. Precipitation and potential evapotranspiration for the months of April, May, and June at this station totaled 44 mm and 180 mm, respectively.

DISCUSSION

Our results show that N and P addition following immobilization with C addition stimulated plant growth, which confirms our expectation. While there is wide agreement that C addition leads to microbial immobilization of N (Jackson et al. 1989, Morgan 1994, Paschke et al. 2000, Blumenthal et al. 2003), the effects of C on P are both mixed and less numerous. Jonasson et al. (1996) observed P reduction from sucrose, but Mazzola et al. (2008) did not, nor did Seastedt and Suding (2007), even after applying gypsum. Others have used calcium to make P unavailable (Belnap et al. 2003). Since an increase in P availability can lead to increased growth and N uptake, causing decreased N availability (Herron et al. 2001), it should be established whether effects and interactions

of P could account for some of the inconclusive literature dealing with suppression of invasives by means of C addition. Additionally, although ample P availability benefits *B. tectorum*, there is little information about the role of P as a possible facilitator of N use.

For soil immobilization to succeed as a means of suppressing weeds that out-compete desirable native grasses, nutrient reduction must persist long enough to preferentially inhibit weeds (Tisdale 1985). *Pseudoroegneria spicata* responded more to N addition in this study than did *B. tectorum*, reinforcing the idea (Stoy et al. 1989) that it might not be an optimum candidate to compete with *B. tectorum* in a low nutrient setting. Indeed, some have found that low N affects annuals and perennials equally (Berendse et al. 1992). Like many invasives, *B. tectorum* is highly competitive—that is, it shows a strong positive growth response— at high nutrient levels (Burke and Grime 1996), but it is also reported to remain nearly so at naturally or artificially low levels (Monaco et al. 2003, Young and Mangold 2008). James (2008) suggested that reducing N levels alone will not favor perennial grasses over annual grasses because natives and invasives display a similar reduction in relative growth rate under increasing N stress. One reason for the divergent observations could be insufficient immobilization, either in magnitude or duration (Reever Morghan and Seastedt 1999, Mangold and Sheley 2008,). Mazzola et al. (2008) saw substantial *B. tectorum* reduction at the C rate we used, but we did not observe more limitation of *B. tectorum* shoot dry mass relative to reduction of *P. spicata* mass, or even a significant N effect at all. In fact, the opposite situation appeared to occur. *B. tectorum* biomass increased slightly less than that of *P. spicata* with P addition, and *B. tectorum* biomass did not react to N addition, while *P. spicata* (and *C. virgata*) each increased 35%. The difference suggests that shoot dry mass in *B. tectorum* was not

as nutrient limited as was mass in *P. spicata* and *C. virgata*. It also suggests that establishing native populations are unlikely to be jeopardized by *C. virgata* recruitment if *B. tectorum* is already firmly established.

This greater relative nutrient sensitivity by the perennial compared to the annual contradicts prevailing hypotheses about competition, but is not unprecedented (Tomlinson and O'Connor 2004). Our R^2 was relatively low for shoot dry mass, showing that other factors were influencing our plants. Possible explanations include the artificial establishment process of transplantation, artifacts and interactions of the starter soil and the soil at the field site, and/or different micronutrient requirements (at least *B. tectorum* may be seasonally Mn-limited, Miller et al. 2006). As a non-leguminous plant, *B. tectorum* might also be able to compensate for low N by producing low-N tissue rather than acquiring more N (Craine et al. 2002), and Weigelt (2005) describes how grass species with high growth rates can uptake more mineral N than slow growers. Finally, *B. tectorum* might have ways of ameliorating its nutrient environment, for it can acquire mycorrhizae quickly in semi-arid systems (Allen 1984). Perhaps this accounts for the increased biomass *B. tectorum* experienced competing with *Hilaria jamesii* relative to itself in monoculture (Belnap and Sherrod 2009). Although *B. tectorum* is generally affected by sucrose (Monaco et al. 2003, Mazzola et al. 2008), if our result commonly occurs in the field, sucrose's efficacy at reducing *B. tectorum* might be highly site-specific, and even counterproductive. *Pseudoroegneria spicata* had less absolute biomass than the other species we studied, but as a slow growing late seral, it can remain competitive (Harpole 2006) when interference is less prevalent at low nutrient availabilities. Plants might grow slightly for several reasons: use of fewer nutrients, low

tissue turnover, and/or high nutrient resorption efficiency (Aerts 1999). It is true that some annual grasses can compete with seedlings or adults of native bunchgrasses (Hamilton et al. 1999), but this should not be a deterrent to seeking the establishment of native populations.

Regardless, species effects on competition did not appear to be important. In one study involving a perennial grass, *B. tectorum* was inhibited more by interspecific competition, while intraspecific competition was more influential on *B. gracilis* (Lowe et al. 2002). *P. spicata* is more inhibited by interspecific competition (Jacobs and Sheley 1999, Seastedt and Suding 2007), but at our nutrient levels, no clear patterns emerged.

The physiological results reflect instantaneous conditions within the plant, rather than a cumulative response to an entire growing season like biomass, and they were measured in rates per unit area. Nevertheless, conditions during data collection were typical of many days in the growing season, with full sun and temperatures around 25 degrees centigrade during measurement, and the results offer a glimpse of the relative activities of specific mixtures under treatment. *Pseudoroegneria spicata* tended to have greater photosynthetic rates than *B. tectorum*. Although photosynthetic N use efficiency would be expected to be greater in *P. spicata* (Link et al. 1995), the greater absolute photosynthetic rates could indicate that times exist when *P. spicata* is more physiologically active, and thus more competitive, than annual invaders. Identifying whether this trend is consistent on a circadian or a seasonal scale could help confirm this possibility. The surprising result, at least compared to the general effect of nutrients on biomass, is that control treatments produced the highest mean photosynthetic rates in *P. spicata* (in monoculture) and *C. virgata* (mixed with *P. spicata*). The lowest means for

these species occurred in the N-only treatment (*P. spicata* monoculture) and N + P treatment (*C. virgata* monoculture). Ionic stress is one possible explanation, and might have occurred in another amendment study (Belnap and Sherrod 2009). In an *A. tridentata*/*P. spicata* community in central Washington, gas exchange processes such as stomatal conductance and photosynthetic rate were strongly related only to time since germination, and only weakly so to N and water (Link et al. 1995). We were unfortunately unable to test this.

Interestingly, there were no significant differences among species treatments or nutrient treatments for either *P. spicata* or *C. virgata* stomatal conductance or transpiration, but there were for *B. tectorum*. The pattern is very similar between the two responses, suggesting that the two processes are closely correlated. The highest rates of *B. tectorum* conductance and transpiration occurred in competition with *P. spicata*, and again the maximum occurred in the control treatment, though it was not statistically different from the next highest (N + P with *P. spicata*), or several others. This suggests that in competition with *P. spicata*, *B. tectorum* tends to transpire more water without an associated gain in photosynthetic output, perhaps owing to more available soil water in these communities. Conversely, *P. spicata* and *C. virgata* photosynthesized more in certain treatments without a significant increase in associated water use (or CO₂ conductance through stomata) in any treatment, which might reflect a drought adaptation. The role of soil water availability in this instance is unknown. We did not control for the availability of soil moisture, but found only that it was not affected by our treatments. However, it is possible that its availability on short time scales could have limited plant growth. For example, addition of a deficient nutrient can actually lead to decreases in

plant tissue concentration of that nutrient because of stimulated growth exceeding nutrient uptake (Daoust and Childers 2004). Fertilization thus might have induced a brief water shortage. Although the soil water content data from late June weakly suggest that the N + P treatment was associated with more water content in the three-species mixture plots, the implications of this are not clear. More available nutrients would be expected to result in increased plant growth and therefore conductance and transpiration, leading to a decrease in soil moisture.

The enormous success (Lacey et al. 1989, Sheley et al. 1998) of Russian, spotted, and diffuse knapweeds (*Centaurea repens*, *C. maculosa*, and *C. diffusa*, respectively) has inspired fears of potentially similar behavior from *C. virgata*. *C. diffusa* apparently invades most readily on fertile sites with no grass competition (Seastedt and Suding 2007). Results are again puzzling, with positive responses reported for diffuse knapweed biomass when receiving N fertilizer, but no reduction following immobilization from C application (Seastedt and Suding 2007). Soil nutrients limit knapweeds in general, which are competitive when nutrients are plentiful (Velagala et al. 1997, Herron et al. 2001), but *P. spicata* only sometimes (Meiman et al. 2006). Being congeneric does not imply too much, because *C. maculosa* and *C. diffusa* appear to have different interactions with the soil biota (Meiman et al. 2006). It is not surprising, then, that *P. spicata* seedlings grew more slowly than *C. virgata* seedlings in our study (Fig. 2.2). Some evidence exists that *C. maculosa* has an allelopathic effect on *P. spicata* (Ridenour and Callaway 2001), but nothing in our study suggested that *C. virgata* exerted a similar effect. Although soil effects and competition do not fully account for the success of *Centaurea* as a group (Blicker et al. 2002), it is difficult to predict invasion potential of *C. virgata* when even

those properties have not been characterized. Whatever its similarities, it certainly has been slower to invade new territory than have other *Centaurea* species, a fact that is somewhat surprising in view of its tolerance for low P levels. This can perhaps be attributed to *P. spicata* competing well against it, or alternatively to a lack of nutrient limitation for other competitors.

Conclusions

In Great Basin soils, low N and P levels can inhibit plant growth after soil C amendment, but in this experiment we did not observe significant effects of neighbor identity except in certain physiological interactions with soil nutrients, and these were inconsistent. This is probably due to differences in available nutrient levels and particular soil conditions. While this fails to confirm findings of some immobilization experiments, it does not preclude the establishment of *P. spicata* with *B. tectorum* and *C. virgata* present; we can expect that establishment with weeds as neighbors will be as likely as in monoculture, because competition was not apparent under our conditions. Our results do not suggest that immobilization and/or nutrient addition preferentially inhibit weeds over *P. spicata*, but confirmation of long-term *P. spicata* survival following establishment in low-nutrient conditions should be a research priority. *Bromus tectorum* is not likely to be eradicated on anything approaching a large scale at a given site, but significant native grass cover, if obtained, will restore some of the function lost to invasions of exotic weeds.

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TABLE 2.1. Three-way factorial analysis of variance on shoot dry mass of A) *Pseudoroegneria spicata*, B) *Bromus tectorum*, and C) *Centaurea virgata*.

A) <i>P. spicata</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	2.01	5.85	0.02
phosphorus	1	1.62	4.72	0.03
nitrogen*phosphorus	1	0.26	0.76	0.39
mix	3	0.16	0.47	0.70
nitrogen*mix	3	0.35	1.01	0.39
phosphorus*mix	3	0.15	0.44	0.73
nitrogen*phosphorus*mix	3	0.08	0.22	0.88
Error	69	0.34		
B) <i>B. tectorum</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.08	0.28	0.60
phosphorus	1	1.08	4.00	0.05
nitrogen*phosphorus	1	0.12	0.44	0.51
mix	3	0.18	0.66	0.58
nitrogen*mix	3	0.29	1.08	0.36
phosphorus*mix	3	0.31	1.14	0.34
nitrogen*phosphorus*mix	3	0.12	0.44	0.72
Error	69	0.27		
C) <i>C. virgata</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	1.84	4.86	0.03
phosphorus	1	0.05	0.13	0.72
nitrogen*phosphorus	1	0.57	1.50	0.23
mix	3	0.70	1.85	0.15
nitrogen*mix	3	0.09	0.25	0.86
phosphorus*mix	3	0.72	1.90	0.14
nitrogen*phosphorus*mix	3	0.23	0.60	0.62
Error	63	0.38		

TABLE 2.2. Three-way factorial analysis of variance on photosynthetic rate of A) *Pseudoreogeneria. spicata*, B) *Bromus tectorum*, and C) *Centaurea virgata*.

A) <i>P. spicata</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	3.11	1.90	0.18
phosphorus	1	0.00	0.00	0.97
nitrogen*phosphorus	1	1.35	0.83	0.37
mix	3	0.33	0.20	0.89
nitrogen*mix	3	4.06	2.48	0.08
phosphorus*mix	3	1.28	0.78	0.51
nitrogen*phosphorus*mix	3	5.72	3.50	0.03
Error	30	1.63		
B) <i>B. tectorum</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.05	0.03	0.87
phosphorus	1	2.42	1.22	0.28
nitrogen*phosphorus	1	2.96	1.49	0.23
mix	3	0.10	0.05	0.98
nitrogen*mix	3	1.19	0.60	0.62
phosphorus*mix	3	0.87	0.44	0.73
nitrogen*phosphorus*mix	3	1.65	0.83	0.49
Error	30	1.99		
C) <i>C. virgata</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.07	0.04	0.84
phosphorus	1	4.08	2.42	0.13
nitrogen*phosphorus	1	1.00	0.60	0.45
mix	3	1.97	1.17	0.34
nitrogen*mix	3	5.10	3.03	0.04
phosphorus*mix	3	1.01	0.60	0.62
nitrogen*phosphorus*mix	3	0.84	0.50	0.69
Error	31	1.69		

TABLE 2.3. Three-way factorial analysis of variance on stomatal conductance of A) *Pseudoroegneria spicata*, B) *Bromus tectorum*, and C) *Centaurea virgata*.

A) <i>P. spicata</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.59	1.47	0.23
phosphorus	1	0.52	1.31	0.26
nitrogen*phosphorus	1	0.28	0.70	0.41
mix	3	0.15	0.38	0.77
nitrogen*mix	3	0.04	0.10	0.96
phosphorus*mix	3	0.47	1.18	0.34
nitrogen*phosphorus*mix	3	0.09	0.23	0.87
Error	30	0.40		
B) <i>B. tectorum</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.26	1.13	0.30
phosphorus	1	0.06	0.24	0.63
nitrogen*phosphorus	1	0.08	0.34	0.56
mix	3	1.40	6.03	0.00
nitrogen*mix	3	0.80	3.44	0.03
phosphorus*mix	3	0.10	0.45	0.72
nitrogen*phosphorus*mix	3	0.98	4.21	0.01
Error	30	0.23		
C) <i>C. virgata</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.00	0.01	0.94
phosphorus	1	0.02	0.03	0.86
nitrogen*phosphorus	1	0.14	0.19	0.67
mix	3	1.29	1.68	0.19
nitrogen*mix	3	0.53	0.69	0.57
phosphorus*mix	3	0.49	0.64	0.60
nitrogen*phosphorus*mix	3	0.40	0.52	0.67
Error	31	0.77		

TABLE 2.4. Three-way factorial analysis of variance on transpiration of A) *Pseudoroegneria spicata*, B) *Bromus tectorum*, and C) *Centaurea virgata*.

A) <i>P. spicata</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.40	1.16	0.29
phosphorus	1	0.51	1.47	0.23
nitrogen*phosphorus	1	0.21	0.62	0.44
mix	3	0.15	0.42	0.74
nitrogen*mix	3	0.04	0.11	0.95
phosphorus*mix	3	0.39	1.14	0.35
nitrogen*phosphorus*mix	3	0.08	0.24	0.86
Error	30	0.34		
B) <i>B. tectorum</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.29	1.45	0.24
phosphorus	1	0.05	0.23	0.63
nitrogen*phosphorus	1	0.03	0.14	0.71
mix	3	1.03	5.09	0.01
nitrogen*mix	3	0.72	3.56	0.03
phosphorus*mix	3	0.12	0.57	0.64
nitrogen*phosphorus*mix	3	0.75	3.73	0.02
Error	30	0.20		
C) <i>C. virgata</i>				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.02	0.03	0.87
phosphorus	1	0.07	0.13	0.72
nitrogen*phosphorus	1	0.12	0.23	0.64
mix	3	0.81	1.50	0.23
nitrogen*mix	3	0.47	0.87	0.47
phosphorus*mix	3	0.38	0.71	0.55
nitrogen*phosphorus*mix	3	0.16	0.29	0.83
Error	31	0.54		

TABLE 2.5. Three-way factorial analysis of variance on soil gravimetric water content in A) May, and B) June.

A) May				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	111.73	1.75	0.19
phosphorus	1	114.28	1.79	0.18
nitrogen*phosphorus	1	7.81	0.12	0.73
mix	6	62.09	0.97	0.45
nitrogen*mix	6	76.71	1.20	0.31
phosphorus*mix	6	26.52	0.42	0.87
nitrogen*phosphorus*mix	6	27.87	0.44	0.85
Error	126	63.83		
B) June				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	8.99	0.59	0.44
phosphorus	1	0.33	0.02	0.88
nitrogen*phosphorus	1	0.93	0.06	0.80
mix	6	15.19	0.50	0.81
nitrogen*mix	6	27.16	0.90	0.50
phosphorus*mix	6	23.79	0.78	0.58
nitrogen*phosphorus*mix	6	59.31	1.95	0.08
Error	126	15.17		

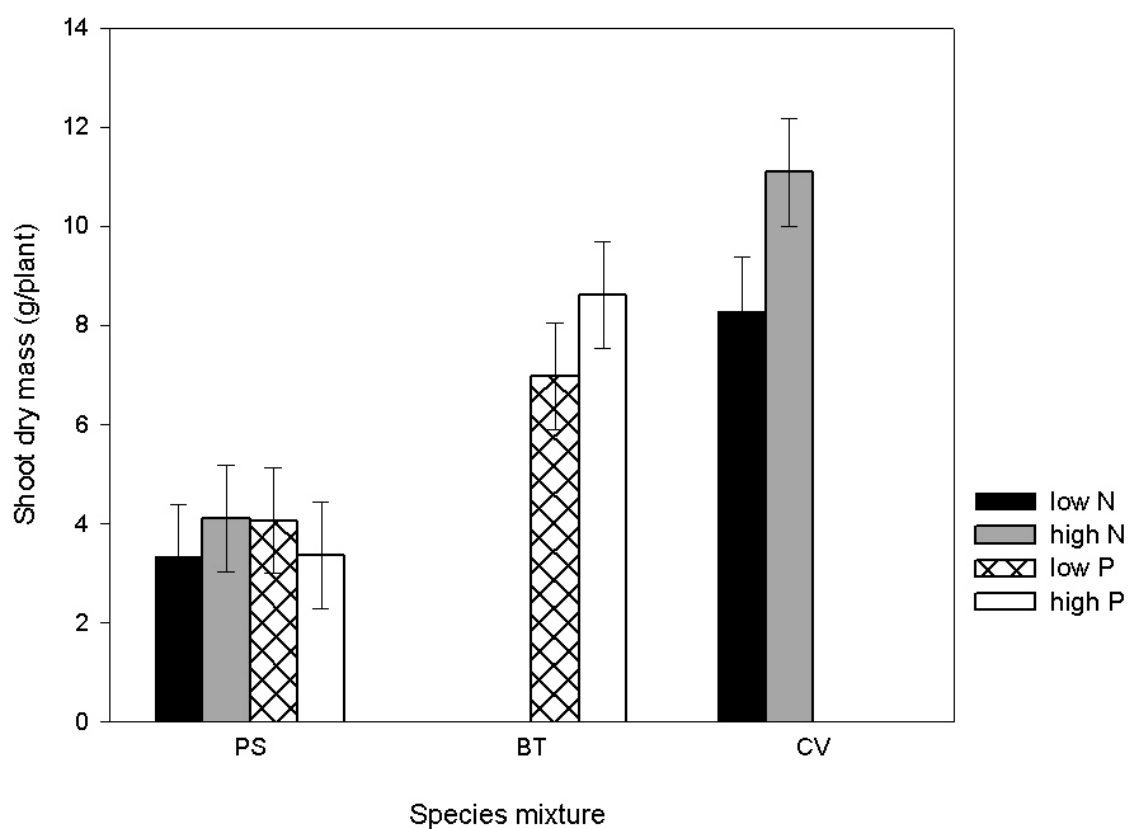


FIGURE 2.1. Significant main effects of nutrient addition on mean (\pm SE) shoot dry mass. Species mixture codes are PS (*Pseudoroegneria spicata*), BT (*Bromus tectorum*), or CV (*Centaurea virgata*). Nutrient treatments (following C addition) are low N (no N added), high N (N added), low P (no P added), and high P (P added). Each species was analyzed separately, thus no mean separations were conducted.

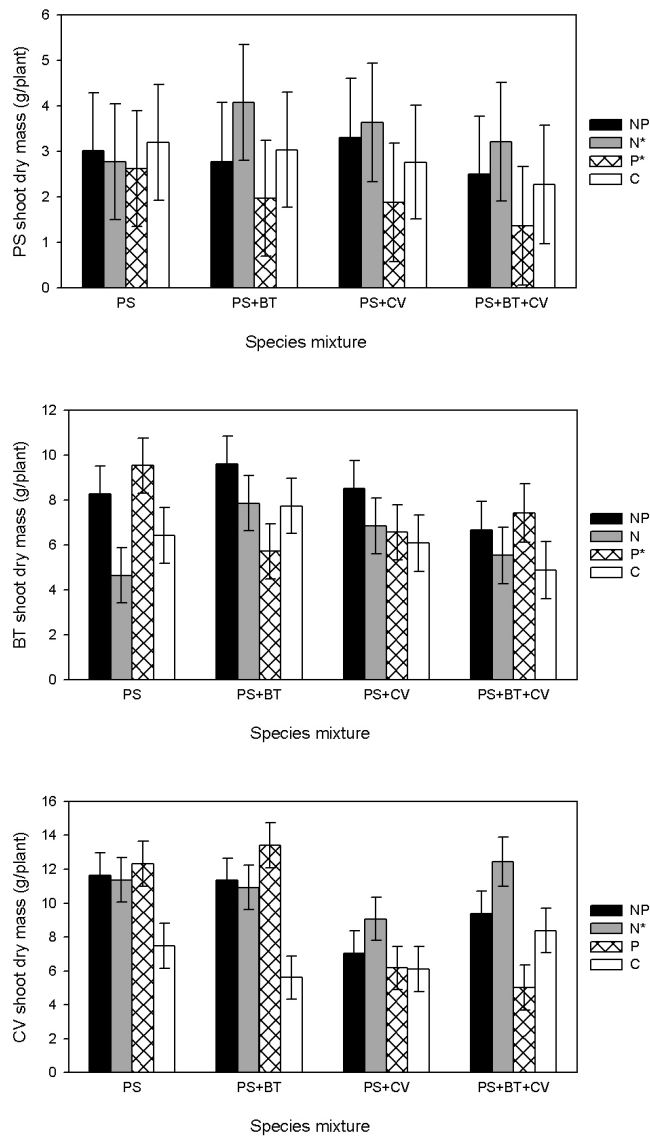


FIGURE 2.2. Relationship of mean (\pm SE) shoot dry mass to species mixture. Species mixture codes are PS (*Pseudoroegneria spicata*), BT (*Bromus tectorum*), CV (*Centaurea virgata*), PS+BT or BT+PS (*P. spicata* and *B. tectorum*), PS+CV or CV+PS (*P. spicata* and *C. virgata*), BT+CV or CV+BT (*B. tectorum* and *C. virgata*), and PS+BT+CV, BT+PS+CV, or CV+PS+BT (*P. spicata*, *B. tectorum*, and *C. virgata*). Nutrient treatments are NP (nitrogen and phosphorus added), N (nitrogen added), P (phosphorus added), and C (no nutrient addition). Asterisks mark significant nutrient main effects.

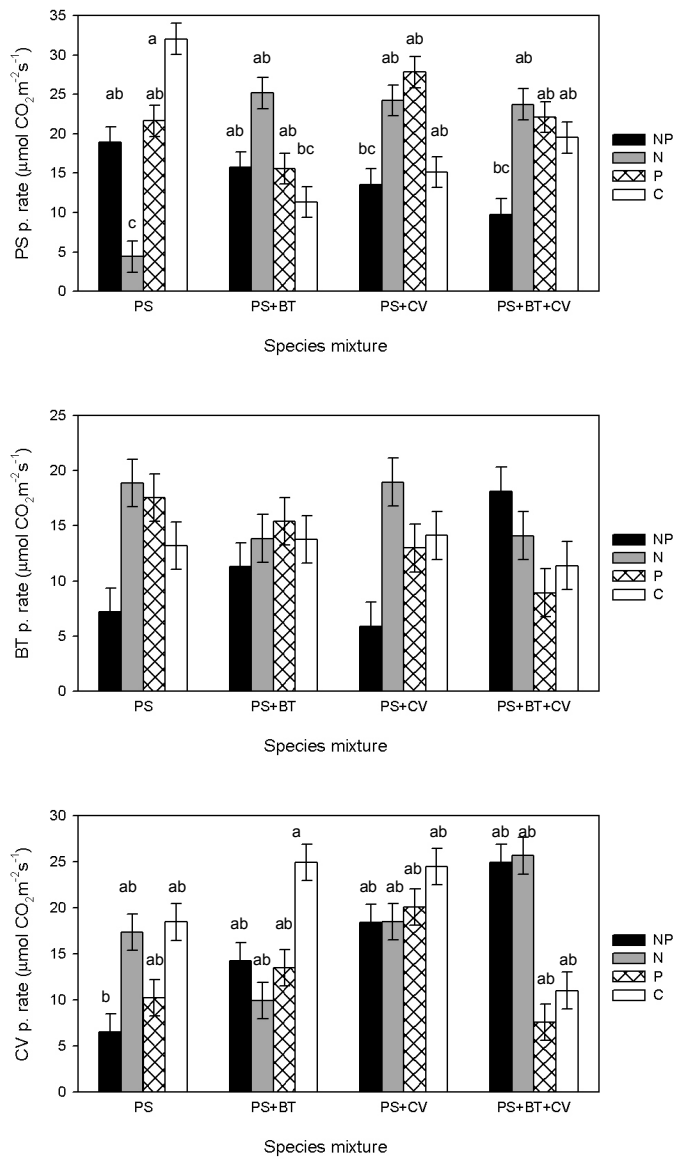


FIGURE 2.3. Relationship of mean (\pm SE) photosynthetic rate to species mixture. Species mixture codes are PS (*Pseudoroegneria spicata*), BT (*Bromus tectorum*), CV (*Centaurea virgata*), PS+BT or BT+PS (*P. spicata* and *B. tectorum*), PS+CV or CV+PS (*P. spicata* and *C. virgata*), BT+CV or CV+BT (*B. tectorum* and *C. virgata*), and PS+BT+CV, BT+PS+CV, or CV+PS+BT (*P. spicata*, *B. tectorum*, and *C. virgata*). Nutrient treatments are NP (nitrogen and phosphorus added), N (nitrogen added), P (phosphorus added), and C (no nutrient addition). Where present, different letter groups denote significantly different means ($P < 0.05$).

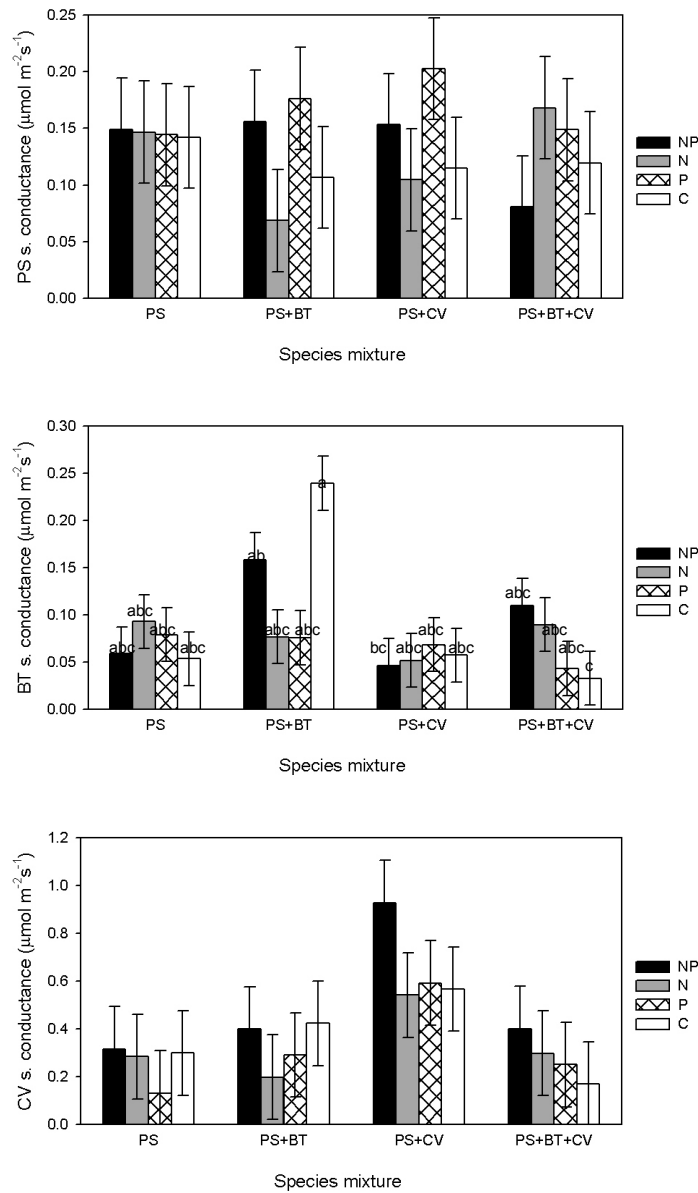


FIGURE 2.4. Relationship of mean (\pm SE) stomatal conductance to species mixture. Species mixture codes are PS (*Pseudoroegneria spicata*), BT (*Bromus tectorum*), CV (*Centaurea virgata*), PS+BT or BT+PS (*P. spicata* and *B. tectorum*), PS+CV or CV+PS (*P. spicata* and *C. virgata*), BT+CV or CV+BT (*B. tectorum* and *C. virgata*), and PS+BT+CV, BT+PS+CV, or CV+PS+BT (*P. spicata*, *B. tectorum*, and *C. virgata*). Nutrient treatments are NP (nitrogen and phosphorus added), N (nitrogen added), P (phosphorus added), and C (no nutrient addition). Where present, different letter groups denote significantly different means ($P < 0.05$).

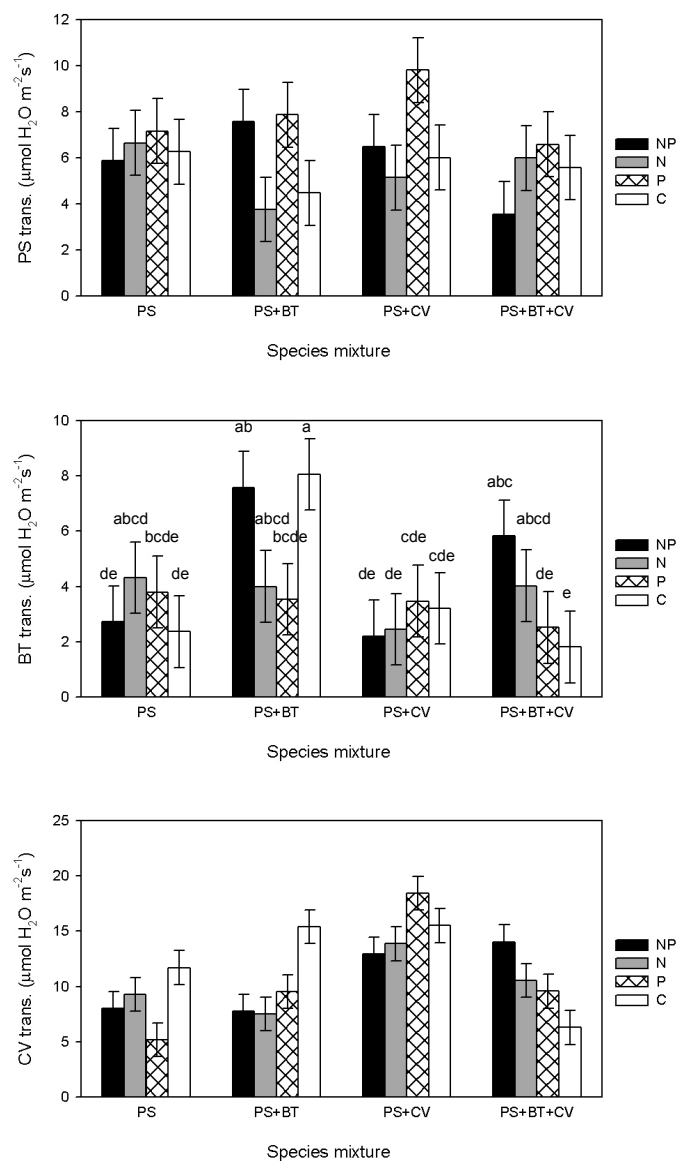


FIGURE 2.5. Relationship of mean (\pm SE) transpiration to species mixture. Species mixture codes are PS (*Pseudoroegneria spicata*), BT (*Bromus tectorum*), CV (*Centaurea virgata*), PS+BT or BT+PS (*P. spicata* and *B. tectorum*), PS+CV or CV+PS (*P. spicata* and *C. virgata*), BT+CV or CV+BT (*B. tectorum* and *C. virgata*), and PS+BT+CV, BT+PS+CV, or CV+PS+BT (*P. spicata*, *B. tectorum*, and *C. virgata*). Nutrient treatments are NP (nitrogen and phosphorus added), N (nitrogen added), P (phosphorus added), and C (no nutrient addition). Where present, different letter groups denote significantly different means ($P < 0.05$).

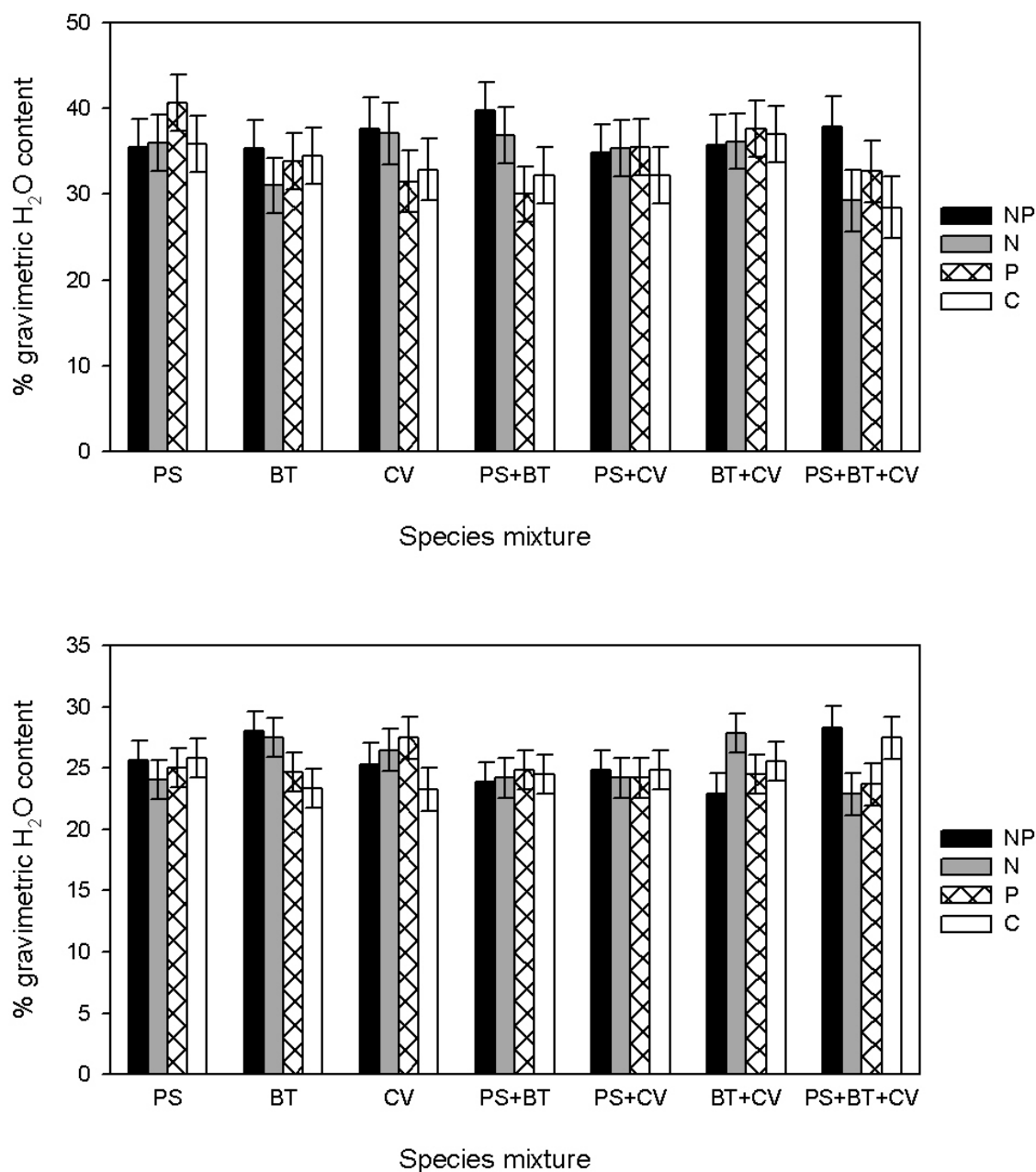


FIGURE 2.6. Relationship of mean (\pm SE) soil gravimetric water content to species mixture. Species mixture codes are PS (*Pseudoroegneria spicata*), BT (*Bromus tectorum*), CV (*Centaurea virgata*), PS+BT (*P. spicata* and *B. tectorum*), PS+CV (*P. spicata* and *C. virgata*), BT+CV (*B. tectorum* and *C. virgata*), and PS+BT+CV (*P. spicata*, *B. tectorum*, and *C. virgata*). Nutrient treatments are NP (nitrogen and phosphorus added), N (nitrogen added), P (phosphorus added), and C (no nutrient addition). Upper figure represents May sampling, lower figure represents June sampling.

CHAPTER 3

NITROGEN AND PHOSPHORUS EFFECTS ON CHEATGRASS, SQUARROSE
KNAPWEED, AND BLUEBUNCH WHEATGRASS GROWN ON A LOW
FERTILITY SOIL

Abstract. The annual invasive grass *Bromus tectorum* and the perennial invasive forb *Centaurea virgata* have demonstrated the ability to exclude more desirable species in the Great Basin of the USA with substantial economic and ecological damage. Because soil resources can affect the outcome of plant-plant interactions, we investigated how these species and the desirable native perennial bunchgrass *Pseudoroegneria spicata* respond to soil nutrients. We factorially applied treatments of low and high nitrogen and phosphorus to each species in monoculture as well as to mixtures of these species. *Bromus tectorum* responded most strongly to nutrient addition, followed by *P. spicata* and then *C. virgata*. The grasses experienced highest growth when receiving both nitrogen and phosphorus. For all species, nitrogen addition induced more growth than either phosphorus addition alone or the control. Each species showed at least some evidence of being interactively affected by N and P, particularly *P. spicata*. *Centaurea virgata* better tolerated low phosphorus than the other species. *Pseudoroegneria spicata* was not relatively more competitive with weeds under low nutrient conditions compared to high nutrient conditions, and was more susceptible to intraspecific than interspecific competition for phosphorus. While the importance of nitrogen in structuring plant communities is already widely recognized, a thorough awareness of the potential for P limitation and P facilitation of nitrogen use is suggested.

INTRODUCTION

Rangeland weeds, including the invasive annual *Bromus tectorum* L. (cheatgrass), lead to an economic loss estimated at two billion dollars annually (DiTomaso 2000), caused in part by increasing incidence of wildfire and reduced productivity (Mack 1981, D'Antonio and Vitousek 1992, Young 1992). *Bromus tectorum* in particular has caused one of the continent's most destructive invasions (Vasquez et al. 2008) and has led to reductions in of the fire return interval in the Great Basin from 30-110 years to 3-5 years (Whisenant 1990). These increased fires have caused substantial changes in vegetation and ecological processes (Pyke et al. 2003). *Centaurea* species are also destructive and are some of the most widespread invaders of North American prairies (LeJeune and Seastedt 2001, Skinner et al. 2000), but at least one member of the genus, *Centaurea virgata* Lam. ssp. *squarrosa* (Willd.) Gugler (squarrose knapweed), has gained a foothold in the heart of the Great Basin in central Utah, USA. It is a short-lived perennial forb capable of forming dense monospecific stands. Reversing or slowing the spread of both weeds has clear benefits, and addressing different aspects of species performance, including resource supply, ecophysiology, stress, and interference, should help in the development of restoration strategies (Krueger-Mangold et al. 2006). Resource fluctuations in general could account for some of the ongoing invasion of the Great Basin by *B. tectorum* (Chambers et al. 2007) and deserve scrutiny.

Invasions are often associated with changes in soil processes (Ehrenfield and Scott 2001). Soil nutrient availability is an important factor in plant communities (Goldberg 1990, Tilman 1990), and N in particular is a major structural driver in many systems (Tilman 1982, Tilman and Wedin 1991, McLendon and Redente 1992). In one

semi-arid system, N was the most limiting nutrient in a *Pseudoroegneria spicata* (Pursh) A. Löve ssp. *spicata* (bluebunch wheatgrass)/*Festuca idahoensis* association; it was more important than water, even in drought (Kreuger-Mangold et al. 2004). Soil N levels are naturally low in many semi-arid ecosystems like the Great Basin (Redente et al. 1992), which in many undisturbed areas is dominated by perennial bunchgrasses in association with *Artemisia tridentata*. Elevated N concentrations resulting from disturbances including fire and managerial interventions (Stubbs and Pyke 2005) typically produce a strong positive response in early-seral invasive species such as *B. tectorum* (Dakheel et al. 1993). Since plants tend to generate feedback loops with the soil that affects nutrient availability (Wedin and Tilman 1990, Hobbie 1992, Radosovich et al. 2007), this can lead to a situation that favors *B. tectorum*, at least in the short term. Increasing *B. tectorum* tends to exclude native establishment, without which ultimate recovery is unlikely (Brooks and Pyke 2001). However, the literature suggests that species with high N requirements should grow more slowly than ones with low N requirements on an N-impooverished soil (Grime 1979), and that late successional natives often respond little to soil nutrient changes (Chapin 1991, Chapin et al. 1993). Therefore, if plants that can persist under the lowest resource condition end up dominating a site (Tilman 1988), *B. tectorum* and other nitrophilic invasives should decrease as soil N becomes less available (Blumenthal 2003). Furthermore, as *P. spicata* is relatively unaffected by soil nutrients in general (Lindquist et al. 1996) and by N in particular compared to knapweed species (Mangold and Sheley 2008), then under low N it should also be expected to successfully compete against *C. virgata*.

Soil P might also constrain plant growth in certain systems (Sharpley 2000), although this has been demonstrated less consistently. McLendon and Redente (1991) did not observe an effect of P on semi-arid succession, but Redente et al. (1992) found that it was potentially as limiting as N in the same systems. P availability in calcareous soils can be limited by the concentrations of carbonates and free Ca^{2+} (Miller et al. 2006). Additionally, P limitation might constrain the rate of N fixation and N bioavailability (Smith 1992), which could lead to important interactions between the two nutrients. In fact, a three-way interaction between N, P, and K was observed in *Poa pratensis* (Ebdon et al. 1999). If P bioavailability tends to peak in summer and winter, rather than in spring and fall (Perrott et al. 1992), then these interactions could be seasonal in nature, possibly affecting some plant types preferentially. Indeed, Miller et al. (2006) found that *B. tectorum* was nutrient-limited in the winter, probably by P and/or Mn, and low P has been associated with strongly reduced emergence of *B. tectorum* (Belnap et al. 2003) as well as generally reduced *B. tectorum* performance (Belnap and Sherrod 2009). Additionally, P has been proposed as a limiting nutrient in systems invaded by *Centaurea* spp., for which they might compete more effectively than existing vegetation (LeJeune and Seastedt 2001).

Soil carbon amendment has received considerable attention as a means to manipulate nutrient availability, especially that of N (Morgan 1994, Paschke et al. 2000, Mazzola et al. 2008). By applying a source of labile C to the soil, usually sucrose or sawdust, the microbial community incorporates it as new biomass and takes up N in the process, reducing N availability to plants (Zink and Allen 1998, Barrett and Burke 2000). Although McLendon and Redente (1991, 1992) succeeded in achieving some control

over annuals with C amendments, other studies have seen mixed results (Morgan 1994, Lowe et al. 2002), specifically finding that natives and *B. tectorum* alike are suppressed (Monaco et al. 2003). Most of this work has focused on N immobilization, although Jonasson et al. (1996) found that sucrose application also immobilized P. It is possible that other micronutrients are also immobilized in such a situation, but in practice most researchers have focused on macronutrients. In any event, soil fertility or the lack thereof could be increasingly transient in time and space, as many ecosystems are experiencing increasing N and P inputs (Vitousek et al. 1997, Bennett et al. 2001), though some semi-arid systems might actually be losing soil nutrients (Evans and Ehleringer 1994). If the relationship between nutrients and differential plant performance were adequately understood, it is possible that managers could exploit alterations in fertility to achieve greater control over invasive weeds and establishment of native species.

Describing the behavior of *P. spicata* in particular is beneficial because locations with large components of *P. spicata* and *Festuca* spp. are among the more resistant sites to *B. tectorum* invasion (Blank et al. 2007), and knowledge of the conditions under which *P. spicata* could successfully establish would be highly valuable. Underlying competitive mechanisms between *P. spicata* and *B. tectorum* have not been characterized fully (Vasquez et al. 2008). In addition, *C. virgata* could influence this dynamic in certain areas, and the early stages of knapweed invasion have not been well studied (Seastedt and Suding 2007). Therefore, we sought to characterize the competitive response of *P. spicata* to *B. tectorum* and *C. virgata*. Our goals were to 1) compare the establishment of monocultures of these three species with the establishment of *P. spicata* in competition with the weeds, reasoning that once established, it is more likely to begin

excluding *B. tectorum* (Humphrey and Schupp 2004) and perhaps *C. virgata*; and 2) simultaneously quantify the effect of soil N and P fertility on these species in monoculture and mixtures. We expected all species to grow more with increasing nutrient availability, but that *P. spicata* would experience a smaller relative increase than the two invasives. We further expected that interspecific competition would be more detrimental to *P. spicata* than intraspecific competition, and we expected a reduction in the degree of competition at lower fertility levels. Although these species compose a relatively simple and artificial community, the structure of Great Basin communities can experience significant consequences from the addition or loss of a single species (Booth et al. 2003). We expected a lower disparity in *P. spicata* performance between high and low levels of soil nutrients compared to the two weeds.

METHODS

Soil and planting

Soil was excavated from near Amalga, Cache County, Utah. This soil was part of the Kidman fine sandy loam series, 0-2% slopes, well drained, with mean annual precipitation of 15-17 inches (Erickson 1974). In December 2007, the soil was dried completely in the Utah State University Research Greenhouse for 3 weeks. The soil was then mixed, and 2800 g (\pm 10 g) was placed in each of 400, 3.8-L pots with approximate diameter of 15 cm. The drainage holes had been previously sealed with heavy-duty tape to prevent the loss of soil, water, and any leachate. Soil sampling at this point indicated 3.4 mg NO₃⁻ kg⁻¹ soil and 5.8 mg available P kg⁻¹ soil (extracted with NaHNO₃). By comparison, a central Washington *A. tridentata* soil had N availability of 26-46 mg kg⁻¹

and P availability of 39-95 mg kg⁻¹ (Meiman et al. 2006). In another study involving a semi-arid western Utah soil with *A. tridentata* and *B. tectorum*, there were 22 mg NO₃⁻ kg⁻¹ and 40-44 mg P kg⁻¹ (Nowak et al. 2006).

Pots were then irrigated to saturation; throughout the experiment, deionized water was used for irrigation to avoid the possibility of hard municipal water tying up available soil P. Pots were sown with at least 10 *C. virgata* seeds that had been personally harvested from the Tintic Valley, Juab County, Utah, approximately 12S 402673 E 4417704 N NAD 83, on 9 Feb 2008. These were followed with at least 10 *P. spicata* P-12 seeds on 15 Feb 2008 that had been purchased from Granite Seed Company, Lehi, Utah. Lastly, on 21 Feb 2008 appropriate pots received at least 10 *B. tectorum* seeds that had been personally harvested from near Vernon, Tooele County, Utah, approximately 12T 385121 E 4441041 N NAD83, then fully after-ripened. The locations of the two harvest sites are separated by roughly 18 miles and 600 feet of elevation. The high sowing rate was employed to assure high capacity for replication. The staggered planting dates were chosen to maximize the likelihood that individuals of the different species would produce more comparable biomass during the establishment period. At least in many cases neighbor size is more important than neighbor identity (Goldberg and Werner 1983).

For germination and early growth the pots received daily irrigation from mid-Feb until 8 Mar 2008 at a rate that kept them visibly moist (50-100 mL). Prior to treatment, pots were thinned randomly and as necessary to produce the mixtures described below. Following treatment implementation, irrigation occurred as necessary to maintain soil gravimetric water content between 8% and 14%. Water content was monitored daily and

exact water additions were calculated by sampling pots from various areas of the greenhouse. Depletion of soil water was primarily a function of specific location within the greenhouse, a conclusion borne out by the results of analyzing total water use over the course of the experiment. Every 6 days, each pot was individually weighed and irrigated to bring it to 14% gravimetric water content, and then randomly reassigned to another location on the benches.

Plant combinations and nutrient treatments

Six different combinations were cultivated. Each consisted of three individuals per pot, one target and two neighbors, because much of the variation in a plant population can be accounted for by interactions with the one or two nearest neighbors (Molofsky 1999). Three monocultures were *B. tectorum*, *C. virgata*, and *P. spicata*. As we were principally concerned with the competitive response of *P. spicata* wheatgrass rather than its competitive effect, it was always the target in the three multi-species mixtures. These were *P. spicata* and *B. tectorum*, *P. spicata* and *C. virgata*, and *P. spicata*, *B. tectorum*, and *C. virgata*. The two-species mixtures contained one target *P. spicata* and two neighbor individuals of the same competitor species, while the three-species mixture had one individual of each species. All plants were marked to ensure the ability to follow individual fates. Targets were chosen near the center of the pot, while neighbors were chosen roughly equidistant and three cm from the target.

Four nutrient treatments were factorially applied using nutrient levels shown to be effective (T. Monaco, *personal communications*). N-only addition consisted of 12.5 mg N/kg soil. Phosphorus-only addition similarly consisted of 12.5 mg P/kg soil. Addition

of N + P consisted of the same amounts of both nutrients, and the final treatment contained only water and no nutrients. Stock solutions were prepared from ammonium nitrate for N treatments and a mixture of mono- and dibasic sodium phosphate (1:140) for P treatments. The small amount of monobasic material was added to preserve relatively neutral pH levels. The pH levels of the soil in question were not significantly altered by addition of the stock solutions (*personal communications*). Treatments were applied 8 Mar 2008.

Data collection and statistical analyses

Grass tiller numbers and *C. virgata* leaf numbers were recorded 30 days after treatment and again at harvest on 9 May 2008, 62 days after treatment. All individuals were harvested and their specific leaf areas and dry shoot biomass were quantified. Separating root biomass to species and individual was not feasible, so total root biomass was washed, dried, and assessed at the pot level in order to test the idea that root systems under low N conditions tend to be proportionally larger (Blicker et al. 2002). All biomass was dried in USU drying ovens. Due to the small size of most individuals, material was dried for 48 h at 40° C. Root dry mass/shoot dry mass quotients were then calculated for all monoculture pots.

All monoculture and mixture treatments had 15 replicates of each of the factorial combinations of nutrients. Except for pot-level variables, only the pre-determined target individuals were analyzed. Final tiller number, final leaf number, specific leaf area, and shoot dry mass were natural log transformed to better meet assumptions of normality, and means and SEs presented here have been back transformed for ease of viewing. Three-

way analyses of variance tested the strength of individual factors on *P. spicata* in mixture and pot-level responses in monoculture, while two-way factorial analyses of variance were used to evaluate the performance of the separate monocultures. Significance was set at $P=0.05$. Least squares mean separations were achieved with Tukey HSD tests, $P=0.05$. All analyses were performed with SAS JMP 7 (SAS 2007). We did not control for alpha across multiple tests due to the relatively small number of responses among monocultures, mixtures, or pots, and a particular interest in interpreting each dependent variable (Moran 2003).

RESULTS

In general, adding N and P to the soil tended to increase growth of all species, as predicted. Soil P became apparently less important to the two invasives with increasing time since treatment. Although this was not universally the case, in no instance did we detect a deleterious effect from nutrient addition.

Response of B. tectorum and C. virgata in monoculture

In *B. tectorum* (Table 3.1), N addition increased 30-day tiller response by 225% ($P<0.01$, Fig. 3.1), 60-day tiller response by 336% ($P<0.01$, Fig. 3.2), specific leaf area (SLA) by 875% ($P<0.01$, Fig. 3.3), and shoot dry mass by 1016% ($P<0.01$, Fig. 3.4; Table 3.1). In each case except 60-day tiller number, the N effect was not independent of P addition (Table 3.1). For example, *B. tectorum* 30-day tillering increased an additional 100% ($P<0.01$) over the N-only treatment when P was also added, despite no effect of P addition alone. A similar pattern was seen with SLA and shoot dry mass, with N + P

addition yielding increases above the N only treatment of 65% ($P<0.04$) and 78% ($P<0.04$), respectively, despite no effect of P alone. At 30 days, *C. virgata* (Table 3.2) had 50% ($P<0.01$, Fig. 3.1) more leaves with added N and P compared to the control, though this differed somewhat from the pattern seen in *B. tectorum*. In addition to the smaller magnitude of the effect, plants required both nutrients to perform differently from the control. Neither N nor P alone conferred any benefit at this stage. After another month, however, P treatment no longer influenced growth of *C. virgata*, either as a main effect or in an interaction. Final leaf numbers (Fig. 3.2), SLA (Fig. 3.3), and dry shoot mass (Fig. 3.4) each responded only to N, with values of 41% ($P<0.01$), 342% ($P<0.01$), and 381% ($P<0.01$), respectively, greater than in the control (Table 3.2).

Response of P. spicata

Pseudoroegneria spicata (Table 3.3) exhibited a pattern similar to 30-day leaf number in *C. virgata*, except the pattern persisted over time. At 30 days (Fig. 3.1), only those plants receiving N and P together had diverged from the control, with a 102% increase ($P<0.01$). Effect magnitude had risen by 60 days (Fig. 3.2) to 173% ($P<0.01$), and the increase was still restricted to joint N and P addition. Additionally, Figs. 3.1 and 3.2 illustrate the Mixture*N interaction ($P=0.04$, $P<0.01$) that occurred in the tillering responses. In Fig. 3.1, the effects of N + P addition just described held for all *P. spicata* mixtures except the two-species mixture with *B. tectorum*, in which N + P addition was not statistically different from P addition (despite clearly trending higher). The situation is less straightforward at 60 days, when the Mix*P interaction was also significant (Table 3.3). Fig. 3.2 shows that in *P. spicata*, tillering did not respond to treatment at all when

grown with *B. tectorum* alone (PS+BT on Fig. 3.2); when grown with *C. virgata* alone (PS+CV on Fig. 3.2) and in the PS+BT+CV pots, only the N effect was significant, and in monoculture, the N + P treatment alone resulted in more growth. Response to N was greatest in mixtures with *C. virgata*, which is interesting in that *C. virgata* itself only responded to N, at least when in monoculture. The *P. spicata* monoculture still displayed the single large spike in the N + P treatment.

Although *P. spicata* was the only species whose tiller or leaf number responded to the N*P interaction by the end of the experiment, its SLA did not respond significantly to any treatment effect (Table 3.3, Fig. 3.3). Larger values for *P. spicata* compared to monocultures of the two invasives are notable. Like the tillering responses, however, shoot dry mass also reflected the action of several interactions (Table 3.3, Fig. 3.4), and these are similar in nature to those of 60-day tillering. Relative to controls, nutrients had smaller effects on *P. spicata* when it was surrounded by interspecific competitors rather than itself; only in monoculture did the N*P interaction make a large difference (594%, $P < 0.02$) over the control, which explains the significant Mix*N*P interaction. Relative to the monoculture, absolute values of *P. spicata* biomass treated with N + P were reduced in both mixtures containing *B. tectorum*. In the *P. spicata* - *B. tectorum* mixture, there was once again no statistical treatment effect, although there was a trend toward an N effect. N addition was significant only in the *C. virgata* mixture, and in the three species mixture, the N + P significantly exceeded only the control.

Response of pot-level variables

Table 3.4 shows ANOVA results for total root dry mass. The first three sets of columns of Fig. 3.5 depict the three species in monoculture, and show familiar patterns. *B. tectorum* stood out both in terms of effect size as well as its absolute per pot values, and under high N conditions appears to have dominated all pots in which it was present. Increases from control to N addition and from N addition to N + P addition were 376% and 112%, 293% and 112%, and 295% and 83%, respectively, for the *B. tectorum* monoculture, the *P. spicata* - *B. tectorum* mixture, and the three-species mixture. *Centaurea virgata*'s response echoed its shoot biomass values and showed only an N effect, while *P. spicata* again failed to exhibit a biomass response to added N without P addition as well. While whole-pot root mass values for *P. spicata* and *C. virgata* were very comparable, it is interesting that *P. spicata* - *C. virgata* mixture pots showed only an N effect and no trace of the N*P interaction so characteristic of *P. spicata*. In N + P treatments, *B. tectorum* monocultures averaged 183% more biomass than *P. spicata* monocultures. The root mass/shoot mass ratio in Fig. 3.6 shows a trend in all three monocultures of relatively more root mass under low N, though the only significant intraspecific effect occurred within *P. spicata* (Table 3.4). Here, the control treatment ratio was 106% greater than the N treatment ($P < 0.01$). Both grasses had greater values than *C. virgata* in the control treatment, but no significant differences were observed between grass species in any treatment. All species exhibited slightly higher (nonsignificant) relative root mass under the N+P treatment than the N treatment. Mixtures containing *B. tectorum* showed a weak trend toward using more water than the others, but no treatment significantly affected water use (Table 3.4, Fig. 3.7).

DISCUSSION

Implications for B. tectorum

Our results confirm that *B. tectorum* exhibits reduced growth in low-N conditions, as expected (McLendon and Redente 1991, Monaco et al. 2003). As predicted, N had a stronger impact on the annual *B. tectorum* than on the perennial species, but is this relative impact enough to influence community dynamics? One reason N immobilization has resulted in limited success (McLendon and Redente 1991, 1992) in controlling *B. tectorum* might be insufficient N reduction. When *B. tectorum* is subjected to low N, it nevertheless continues to compete well for N (Monaco et al. 2003, Young and Mangold 2008), which could result in persistence rather than displacement by native perennials. Even when early seral species compete poorly for N, they can compensate with high growth rates and seed production (Tilman and Wedin 1991). This absence of suppression under low-N conditions has led some to conclude that soil N manipulation holds little promise for controlling *B. tectorum* (Reever Morghan and Seastedt 1999, James 2008). Some of this work has concentrated on comparing N uptake rates (Pickett et al. 1987) of invasives like *B. tectorum* and more desirable species and has provided inconsistent results (Paschke et al. 2000, Herron et al. 2001). Further, James (2008) found that natives and invasives experienced similar reductions in relative growth rate under increasing N stress. These results notwithstanding, we observed *B. tectorum* gain a large biomass advantage over the other monocultures in our experiment at high N, while values at low N were much more similar. If N and P, or at the very least P, could be held sufficiently low, results of shoot dry mass suggest that *P. spicata* could indeed survive amidst *B.*

tectorum, and the chances of *B. tectorum* generating the necessary fuel to carry fires that are hot enough to kill establishing natives would be reduced (Brooks and Pyke 2001).

It is not surprising that low P availability also retards growth (Herron et al. 2001), but the N*P interaction we repeatedly observed with tiller number, dry shoot mass, SLA, and total root biomass suggests that a certain amount of P is necessary for optimum growth. This pattern has been seen by others (Craine et al. 2008). Although ample P availability benefits *B. tectorum*, there is little information about the role of P as a possible facilitator of N use. If P does in fact facilitate N uptake, it is possible that P uptake rates could offer increased ability to predict native performance and to choose plant materials more likely to successfully compete against *B. tectorum*. Clearly, any possibility of P mediating competition for N will depend on the particular soil characteristics of a given site and the P availability through time, and only recently have investigators begun observing both macronutrients simultaneously. Phosphorus is generally less mobile than N in soil (Fenn et al. 1998). In the field, only situations in which P is a limiting nutrient would offer the potential to test this possibility, but the smaller body of research on the effects of P on Great Basin plant communities indicates that the extent to which P might be limiting is not well understood and should be explored. Indeed, if P availability changes significantly with C addition (Jonasson 1996), then it is possible that several N-immobilization studies ignored P effects.

Regardless of the particular element, *B. tectorum* tends to assimilate soil nutrients and reach phenological maturity earlier than native perennial grasses (Grotkropp and Rejmanek 2007). Increased shoot dry biomass and SLA under high-P conditions like the

ones in our study likely drive some of these effects. SLA can be an important aspect of relative growth rate in plants (Leishman et al. 2007), and like biomass, we saw it decrease when nutrients were withheld, in accordance with Taub (2002). Additionally, the observed increase in early tillering could facilitate more flowering and ultimately seed production, and if this condition were to lead to increased propagule pressure on perennials in the future, native establishment could drop (Reever Morghan and Seastedt 1999, Mazzola et al. 2008). Although the P interaction on tillering disappeared by the final measurement, it is of interest whether or not seed production would be affected in the field.

Implications for C. virgata

Similar to other knapweeds (Mangold and Sheley 2008), *C. virgata* responded to N manipulation. In low-N treatments, it produced similar levels of shoot dry mass as other species and mixtures, but at high N its biomass was comparable to N + P-*P. spicata* and high N-*B. tectorum*, and only high N + P-*B. tectorum* exceeded it. However, planting *C. virgata* prior to *B. tectorum* probably played a role in the similarity of these values. The fact that P only mattered to *C. virgata* at the earliest stages of rosette formation makes it unlikely that either grass would pose a competitive threat to it for P. The *P. spicata* biomass data bears out LeJeune and Seastedt's idea (2001) that competition for P could potentially mediate the interaction between these species, because *P. spicata* simply does not increase unless both nutrients are available. As a sometimes short-lived perennial forb, it is likely that *C. virgata* could grow fairly slowly during the establishment phase, accumulating nutrients and bolting in a subsequent growing season

(Lacey 1986). Regardless of the low shoot dry biomass, *C. virgata* can and does persist in areas with dense *B. tectorum* cover (Nowak et al. 2006). Our results suggest one reason this could happen is the relative lack of sensitivity to soil P compared to the two potential competitors. Rosette leaf number at 30 days was the only measured trait affected by P, which combined with N to increase response compared to all other treatments. The disappearance of all main effects of P and interactions in the final metrics of leaf number, shoot dry mass, and specific leaf area suggests that *C. virgata* might have exceptionally low P requirements and could behave as a stress tolerator (Grime and Campbell 1991) with regard to P. While this trait seems to be an exception to the pattern of *Centaurea* species utilizing high nutrient availabilities and the absence of grass competition to invade new sites (Seastedt and Suding 2007), it would be a clear advantage coexisting with *B. tectorum* and *P. spicata* in a P-limited system. Diffuse knapweed (*Centaurea diffusa*) exhibited a similar response to low P (Suding et al. 2004).

Spotted knapweed (*Centaurea maculosa*) has been screened for possible allelopathic effects, with some positive evidence (Callaway and Ashehoug 2000), including on the late seral *F. idahoensis* (Ridenour and Callaway 2001). However, others have concluded that interference and allelopathy are not prominent features of the relationship between *C. maculosa* and natives (Suding et al. 2004, Mangold and Sheley 2008), and speculate that they can coexist because of different niches. Although we did not test for the production or uptake of any likely allelopathic chemicals, our results also fail to strongly suggest that any such activity occurred during this experiment, even though our sandy soil with very little organic matter should have facilitated any allelopathic activity (Mangold and Sheley 2008). If anything, *C. virgata* might have

facilitated growth of *P. spicata*, as the latter's 60-day tiller number and shoot dry mass was on average equivalent in non-P treatments, which did not happen with *P. spicata* in monoculture.

Implications for P. spicata

It is important to distinguish that we did not specifically test *P. spicata* as a means of controlling *B. tectorum*. Instead, we sought conditions that would result in roughly equivalent performance, if nothing else, which would at least imply the possibility of native establishment. So despite Lowe et al. (2002) finding that *Bouteloua gracilis* did not gain relative to *B. tectorum* at low N, they did see a greater percent reduction in *B. tectorum* relative to the perennial, which is also what we observed. Even at the low densities we created, competition still occurred, and results depended on nutrient treatment. With added N + P, *P. spicata* was inhibited more by inter- than intra-specific competition, as we expected. When one or more nutrients was absent, *P. spicata* growth was either statistically comparable or even slightly increased when in a multi-species mixture; although this is no guarantee of establishment, at least it makes its prospect reasonable. *B. tectorum* caused more interference than did *C. virgata* (Figs. 3.2, 3.4) and clearly poses a threat to interfere with *P. spicata* during establishment if nutrients are relatively high. If *C. virgata* did in fact ameliorate the P environment for *P. spicata* (see previous paragraph), this might account for some of the difference, and would imply that native establishment is more likely in a dense population of *C. virgata* rather than *B. tectorum*, which we have observed in at least one pair of sites in Tooele County, Utah (unpublished data). As Caldwell et al. (1991) were able to correlate dry shoot biomass of

P. spicata with competition for P, higher soil P availabilities associated with certain types of interspecific competition would appear to raise the chances of successful establishment.

Comparing monoculture responses of *B. tectorum* with those of *P. spicata* (Fig. 3.3), it appears that *P. spicata* is at least in one respect relatively more dependent on P: by 60 days, the difference between control and N + P treatments for *P. spicata* tiller number had increased compared to 30 days, whereas the same trait in *B. tectorum* was not affected by P at 60 days. Although P still exerted a main effect on *P. spicata* shoot dry mass, it was not as strong as the effects of N on these traits. An increasing ability to tolerate low P availability would be consistent with widely recognized properties of the species (Goldberg 1990, Meiman et al. 2006). Even tiller recruitment alone might be associated with more important ramifications down the road, as tiller reductions lead to decreased seed output (Monaco et al. 2003), affecting fitness, and tiller rate strongly influenced persistence of *Agropyron cristatum* in one study (Francis and Pyke 1996). Because N is the strongest stimulator of lateral bud outgrowth in bunchgrasses (Tomlinson and O'Connor 2004), it is somewhat surprising that this particular trait was more affected by P interactions than the others. Another possibility is that early P availability led to increased N uptake and therefore N depletion and subsequent N limitation, which has been observed in communities involving *P. spicata*, *C. maculosa*, and *Elymus elymoides* (Herron et al. 2001).

On the other hand, species mixture effects appear to cause *P. spicata* to behave in a contradictory manner. The strong N * P interaction on tiller number was still observed, and mixture also interacted (independently) with both nutrients on the tiller response.

But P was more influential in this situation, and the monoculture was the only environment that saw substantial reduction in final tiller number without P addition. This makes sense in light of the *C. virgata* results, which indicated that *C. virgata* did not take advantage of P. If *C. virgata* requires low amounts of P and *P. spicata* absolutely requires ample P in order to benefit from increased N, intraspecific competition should be more important when *C. virgata* is the only competitor in the area. In the Mix*N interaction with tiller number, interspecific competition had the more detrimental effect on *P. spicata*. *C. virgata* and *P. spicata* have very different life forms, and herbaceous monocots tend to devote a larger portion of their resources to roots relative to leaves compared to herbaceous dicots (Garnier 1991). Still, and unlike bunchgrasses, *C. virgata* forms a deep taproot that can extend down to ten feet (Scott Jensen, *personal communication* 2001), which would presumably supply access to moisture deeper in the soil profile than *P. spicata* could reach. If in addition to this greater access to soil water *C. virgata* could also tie up N, *P. spicata* could be relatively less likely to establish in such a setting. If N is not limiting, then the *C. virgata* mixture does not appear likely to provide as much competition as *B. tectorum*, although significant competition with *P. spicata* is still possible (Prather and Callahan 1991, Velagala et al. 1997). By the end of the experiment, *P. spicata* tiller numbers in N + P treatments were significantly lower in the *B. tectorum* mixture than in *P. spicata* monoculture or the mixture with *C. virgata*.

The question of whether any advantage is conferred by rapid early growth that does not necessarily result in different biomass at maturity is intriguing, and has been investigated recently in terms of SLA. In general, high SLA is associated with invasive species (Grotkopp et al. 2002) and could be an important pre-adaptation for invading new

habitat (Pysek and Richardson 2007). Furthermore, invasive species tend to have larger values of photosynthetic rate, stomatal conductance, and transpiration (Cavaleri and Sack 2010, Henery et al. 2010). For invasive and native species, more efficient resource use should reduce SLA (Kittelson et al. 2008). Thus the significant reductions for the weeds seen in Fig. 3.3 suggest that *B. tectorum* and *C. virgata* become increasingly efficient at low nutrient levels, while SLA of *P. spicata*—although it had a higher value in every treatment than either weed—remained almost unchanged at different concentrations. Which strategy is evidence of superior competitive ability? Cavaleri and Sack (2010) warn that data obtained from individual leaves do not always—or even often—scale up to the level of a plant or population. For instance, Henery et al. (2010) found that North American specimens of *Centaurea stoebe* (an invasive forb in North America) benefited from a lower SLA relative to Eurasian specimen, contrary to expectation, and was possibly a result of less dissected leaves adapted to a hotter and drier climate. Notably, these different SLA values did not result in significant differences in plant biomass at maturity, leading them to speculate that rapid early growth still conferred a life history advantage (Henery et al. 2010). A similar situation is possible with *C. virgata*, because its juvenile rosettes tend to have leaves with much less dissection compared to mature individuals. It is feasible that this adaptation in young individuals could contribute to the strong reduction in *C. virgata* SLA seen in Fig. 3.3 under low N conditions. While true that low SLA is not always disadvantageous relative to neighboring plants (Leishman et al. 2010), and in some cases has proved a distinct advantage (Henery et al. 2010), whether low SLA is correlated with the tendency of *C. virgata* or *B. tectorum* to invade needs further investigation.

When competition is taken into account, the prime goal of native perennial grass establishment (McLendon and Redente 1992) is difficult. Indeed, increased fertility has been shown to lead to increased susceptibility to invasion (Huenneke et al. 1990), and high N availability is commonly associated with increased weed performance (Burke and Grime 1996, Blumenthal et al. 2003). Over the long run, *B. tectorum* presence has been associated with changes in the availability of soil N and P (Evans et al. 2001, Booth et al. 2003). While this condition could very well be related to the soil biota, it is apparently not a result of arbuscular-mycorrhizal fungi (Rowe and Brown 2008). It is likely that the precise competitive ability of bunchgrasses like *P. spicata* will change with the N:P ratio of any given soil, leading to varying degrees of success in establishment. Although Craine et al. (2008) caution against using N:P ratios as absolute guides to soil fertility, they do note that P can be limiting at even relatively low N:P ratios.

Pot-level responses

The pot-level responses in Fig. 3.5 are interesting in that they reflect in large part the general patterns observed by the species in monoculture. For root dry mass, mixtures containing *B. tectorum* show the partial P-limitation indicated by the large reaction to N that is augmented considerably when P is also added. *Centaurea virgata* monocultures only responded significantly to N, and *P. spicata* biomass remained very low unless N and P were both supplied. Thus, *C. virgata* might not mimic the behavior of *C. maculosa*, against which *P. spicata* was more competitive (Herron et al. 2001). Overall, total *B. tectorum* root mass was substantially greater than in the other species at higher N levels, and we propose that this larger biomass can help explain why an early seral like *B.*

tectorum can remain competitive with perennial natives at nutrient levels lower than has been hoped. Root mass/shoot mass ratios in Fig. 3.7 suggest that efficient shoot biomass production may be one reason. *Pseudoroegneria spicata* is generally considered to be more efficient, slower growing, and late seral compared to *B. tectorum*, yet the two species had statistically equivalent root-shoot ratios. While coexistence cannot be ruled out, given *B. tectorum*'s greater overall root mass, a below-ground competitive advantage for *P. spicata* seems unlikely.

Conclusions

Without considering competition, fertility increases clearly benefitted all species and could lead to greater establishment in similar conditions. Although the strength of nutrient effects was highest in the grasses, these effects depended in some degree on having both soil nutrients present in high quantities. In general, *C. virgata* only increased with N, a result consistent with other knapweed species. *Centaurea virgata* appears to potentially have lower nutrient requirements than either *C. diffusa* or *C. maculosa*, two of the other more commonly studied knapweed species, and did not show strong evidence for possible allelopathy or other interference mechanisms. Although no one factor is likely to fully account for the success of *Centaurea*, it is difficult to predict invasion potential of *C. virgata* when properties such as soil effects and competition have not been characterized. Whatever its similarities to other knapweeds, it certainly has been slower to invade new territory than have some other *Centaurea* species, a fact that is somewhat surprising in view of its tolerance for low soil P levels. This can perhaps be attributed to *P. spicata* competing well against it, or alternatively to a lack of nutrient limitation for

other competitors. We recognize that while most research has focused on reducing fertility rather than adding it, our approach establishes that P limitation can occur, and might reasonably be expected to exist in the field. It is unlikely that N is the sole driver of invasion in semi-arid areas, so we recommend further study of nutrient co-limitation in the Great Basin to help facilitate fundamental understanding of ecosystem processes.

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TABLE 3.1. Results of 2-way factorial ANOVA on growth of *Bromus tectorum* in monoculture. Significant *P*-values and associated factors in bold.

Tiller number, 30 days				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	114.82	129.28	<0.01
phosphorus	1	30.82	34.70	<0.01
nitrogen*phosphorus	1	22.82	25.69	<0.01
Error	56	0.89		
Tiller number, final				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	15.88	253.07	<0.01
phosphorus	1	0.17	2.74	0.10
nitrogen*phosphorus	1	0.00	0.00	1.00
Error	56	0.06		
Specific leaf area				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	65.31	585.44	<0.01
phosphorus	1	1.78	15.96	0.00
nitrogen*phosphorus	1	0.51	4.59	0.04
Error	56			
Shoot dry mass				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.80	270.70	<0.01
phosphorus	1	0.06	20.40	<0.01
nitrogen*phosphorus	1	0.06	21.21	<0.01
Error	56	0.00		

TABLE 3.2. Results of 2-way factorial ANOVA on growth of *Centaurea virgata* in monoculture. Significant *P*-values and associated factors in bold.

Tiller number, 30 days				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	101.40	35.08	<0.01
phosphorus	1	52.27	18.08	<0.01
nitrogen*phosphorus	1	86.40	29.89	<0.01
Error	56	2.89		
Tiller number, final				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	212.82	33.14	<0.01
phosphorus	1	0.02	0.00	0.96
nitrogen*phosphorus	1	20.42	3.18	0.08
Error	56	6.42		
Specific leaf area				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	23.13	100.31	<0.01
phosphorus	1	0.77	3.32	0.07
nitrogen*phosphorus	1	0.01	0.05	0.83
Error	56	12.91		
Shoot dry mass				
Source	DF	MS	<i>F</i>	<i>P</i>
nitrogen	1	0.41	61.07	<0.01
phosphorus	1	0.01	1.22	0.27
nitrogen*phosphorus	1	0.01	1.08	0.30
Error	56	0.01		

TABLE 3.3. Results of 3-way factorial ANOVA on growth of *Pseudoroegneria spicata* in various mixtures. Significant *P*-values and associated factors in bold.

Tiller number, 30 days post-treatment				
Source	DF	MS	<i>F</i>	<i>P</i>
mix	3	1.77	1.15	0.33
nitrogen	1	113.86	74.01	<0.01
mix*nitrogen	3	4.43	2.88	0.04
phosphorus	1	68.70	44.66	<0.01
mix*phosphorus	3	2.37	1.54	0.21
nitrogen*phosphorus	1	44.70	29.06	<0.01
mix*nitrogen*phosphorus	3	1.79	0.39	0.76
Error	218	1.54		
Tiller number, final				
Source	DF	MS	<i>F</i>	<i>P</i>
mix	3	0.42	2.85	0.04
nitrogen	1	14.84	99.75	<0.01
mix*nitrogen	3	0.93	6.27	0.00
phosphorus	1	3.72	25.03	<0.01
mix*phosphorus	3	0.72	4.87	0.00
nitrogen*phosphorus	1	1.98	13.28	0.00
mix*nitrogen*phosphorus	3	0.30	2.03	0.11
Error	213	0.15		
Specific Leaf Area				
Source	DF	MS	<i>F</i>	<i>P</i>
mix	3	0.20	0.40	0.75
nitrogen	1	0.20	0.57	0.45
mix*nitrogen	3	0.20	1.57	0.20
phosphorus	1	0.20	0.83	0.36
mix*phosphorus	3	0.20	0.70	0.55
nitrogen*phosphorus	1	0.20	0.92	0.34
mix*nitrogen*phosphorus	3	0.20	1.95	0.12
Error	3	0.33		
Shoot dry mass				
Source	DF	MS	<i>F</i>	<i>P</i>
mix	3	0.01	2.78	0.04
nitrogen	1	0.31	119.77	<0.01
mix*nitrogen	3	0.00	1.77	0.15
phosphorus	1	0.04	14.50	0.00
mix*phosphorus	3	0.01	4.14	0.01
nitrogen*phosphorus	1	0.01	4.94	0.03
mix*nitrogen*phosphorus	3	0.01	3.52	0.02
Error	213	0.00		

TABLE 3.4. Results of 3-way factorial ANOVA on pot-level responses. Significant *P*-values and associated factors in bold.

Total pot root dry mass				
Source	DF	MS	<i>F</i>	<i>P</i>
mix	5	30.01	28.26	<0.01
nitrogen	1	379.84	357.72	<0.01
mix*nitrogen	5	19.83	18.67	<0.01
phosphorus	1	49.95	47.04	<0.01
mix*phosphorus	5	5.20	4.90	0.01
nitrogen*phosphorus	1	42.42	39.95	<0.01
mix*nitrogen*phosphorus	5	4.23	3.98	0.02
Error	335	1.06		
Root dry mass / shoot dry mass				
Source	DF	MS	<i>F</i>	<i>P</i>
species	2	9.27	30.19	<0.01
nitrogen	1	6.38	20.77	<0.01
species*nitrogen	2	0.82	2.66	0.07
phosphorus	1	0.25	0.80	0.37
species*phosphorus	2	0.12	0.39	0.67
nitrogen*phosphorus	1	0.70	2.29	0.13
species*nitrogen*phosphorus	2	0.32	1.05	0.35
Error	167	0.31		
Total pot water use				
Source	DF	MS	<i>F</i>	<i>P</i>
mix	5	391431.86	1.87	0.10
nitrogen	1	69778.20	0.33	0.56
mix*nitrogen	5	343088.18	1.64	0.15
phosphorus	1	84088.90	0.40	0.53
mix*phosphorus	5	152922.44	0.73	0.60
nitrogen*phosphorus	1	381681.30	1.83	0.18
mix*nitrogen*phosphorus	5	336469.28	1.61	0.16
Error	336	70244432.00		

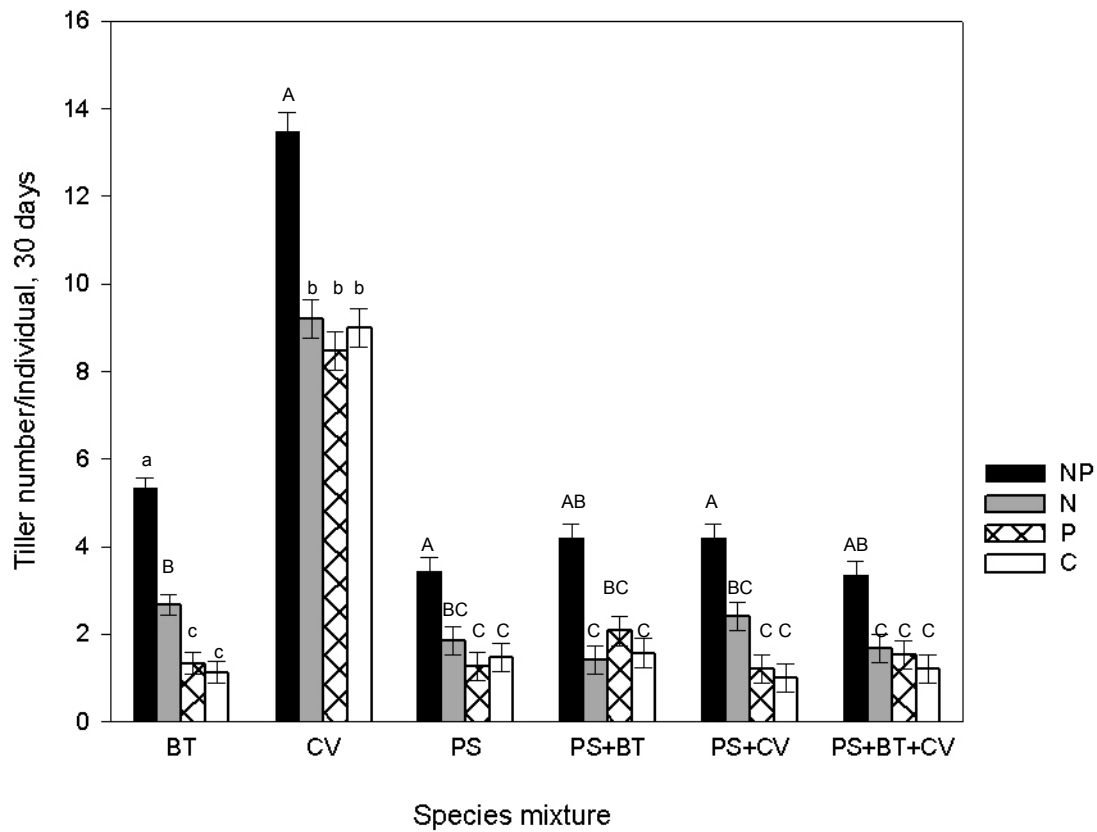


FIGURE 3.1. Relationship of mean (\pm SE) tiller number or leaf number (CV only) to species mixture at 30 days post-treatment. Treatment codes are C, control; P, phosphorus added; N, nitrogen added; and NP, both nutrients added. Species mixture codes across the horizontal axis are BT, *Bromus tectorum* monoculture; CV, *Centaurea virgata* monoculture; PS, *Pseudoroegneria spicata* monoculture; PS+BT, *P. spicata* surrounded by *B. tectorum*; PS+CV, *P. spicata* surrounded by *C. virgata*; and PS+BT+CV, *P. spicata* surrounded by *B. tectorum* and *C. virgata*. Different lower case letters represent significant differences ($P \leq 0.05$) within a given invasive monoculture, and uppercase letters represent significant differences ($P \leq 0.05$) among all pots with a *P. spicata* target.

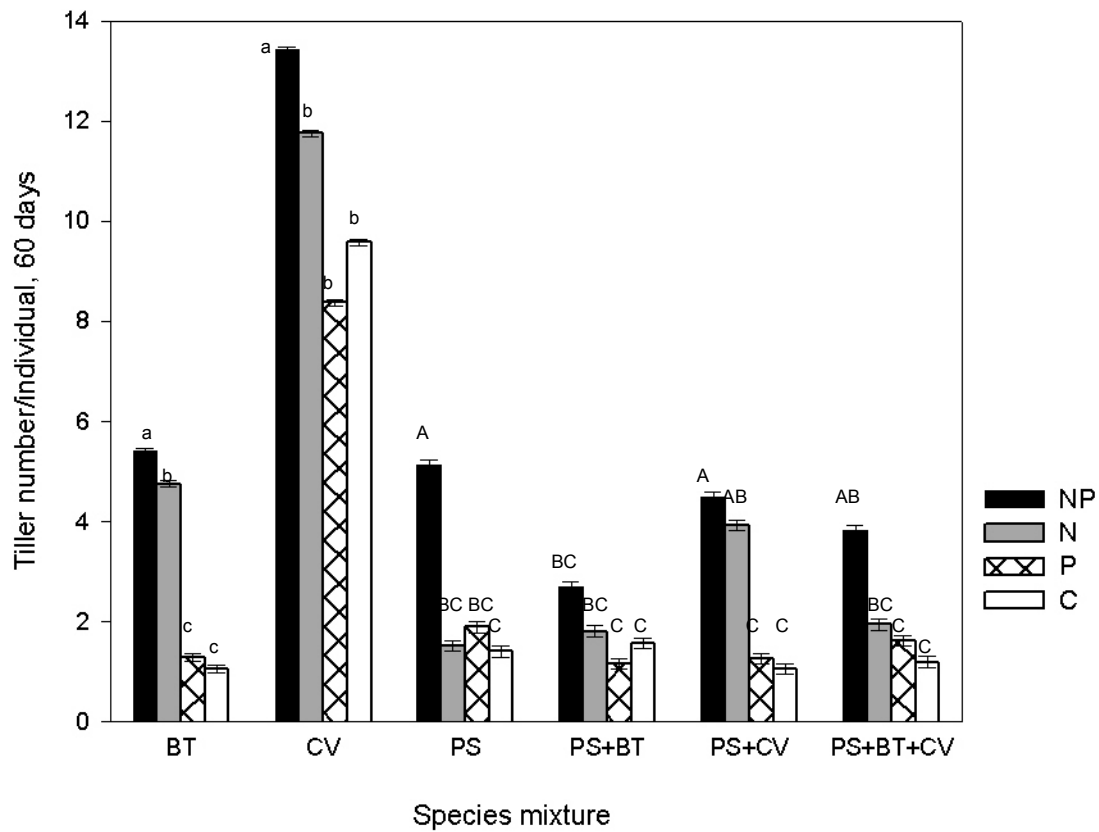


FIGURE 3.2. Relationship of mean (\pm SE) tiller number or leaf number (CV only) to species mixture at 60 days post-treatment, immediately prior to harvest. Treatment codes are C, control; P, phosphorus added; N, nitrogen added; and NP, both nutrients added. Species mixture codes across the horizontal axis are BT, *Bromus tectorum* monoculture; CV, *Centaurea virgata* monoculture; PS, *Pseudoroegneria spicata* monoculture; PS+BT, *P. spicata* surrounded by *B. tectorum*; PS+CV, *P. spicata* surrounded by *C. virgata*; and PS+BT+CV, *P. spicata* surrounded by *B. tectorum* and *C. virgata*. Different lower case letters represent significant differences ($P \leq 0.05$) within a given invasive monoculture, and uppercase letters represent significant differences ($P \leq 0.05$) among all pots with a *P. spicata* target.

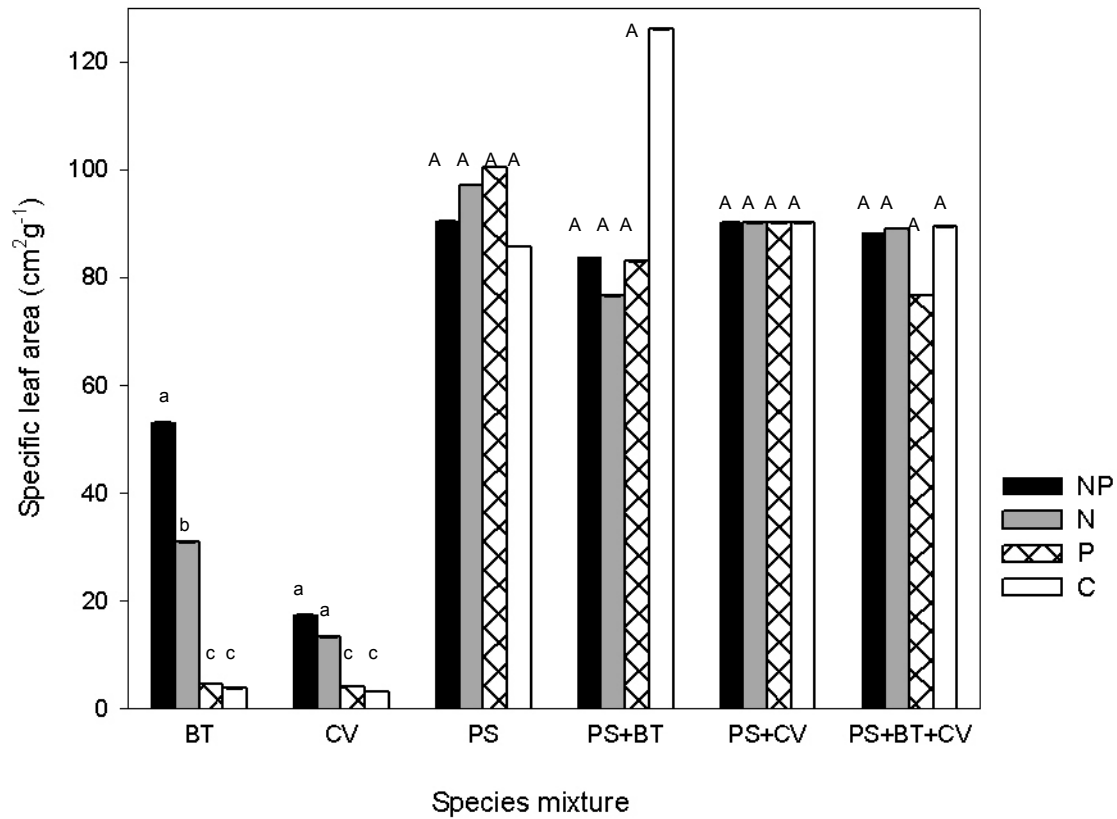


FIGURE 3.3. Relationship of mean (\pm SE) specific leaf area to species mixture at harvest. Treatment codes are C, control; P, phosphorus added; N, nitrogen added; and NP, both nutrients added. Species mixture codes across the horizontal axis are BT, *Bromus tectorum* monoculture; CV, *Centaurea virgata* monoculture; PS, *Pseudoroegneria spicata* monoculture; PS+BT, *P. spicata* surrounded by *B. tectorum*; PS+CV, *P. spicata* surrounded by *C. virgata*; and PS+BT+CV, *P. spicata* surrounded by *B. tectorum* and *C. virgata*. Different lower case letters represent significant differences ($P \leq 0.05$) within a given invasive monoculture, and uppercase letters represent significant differences ($P \leq 0.05$) among all pots with a *P. spicata* target.

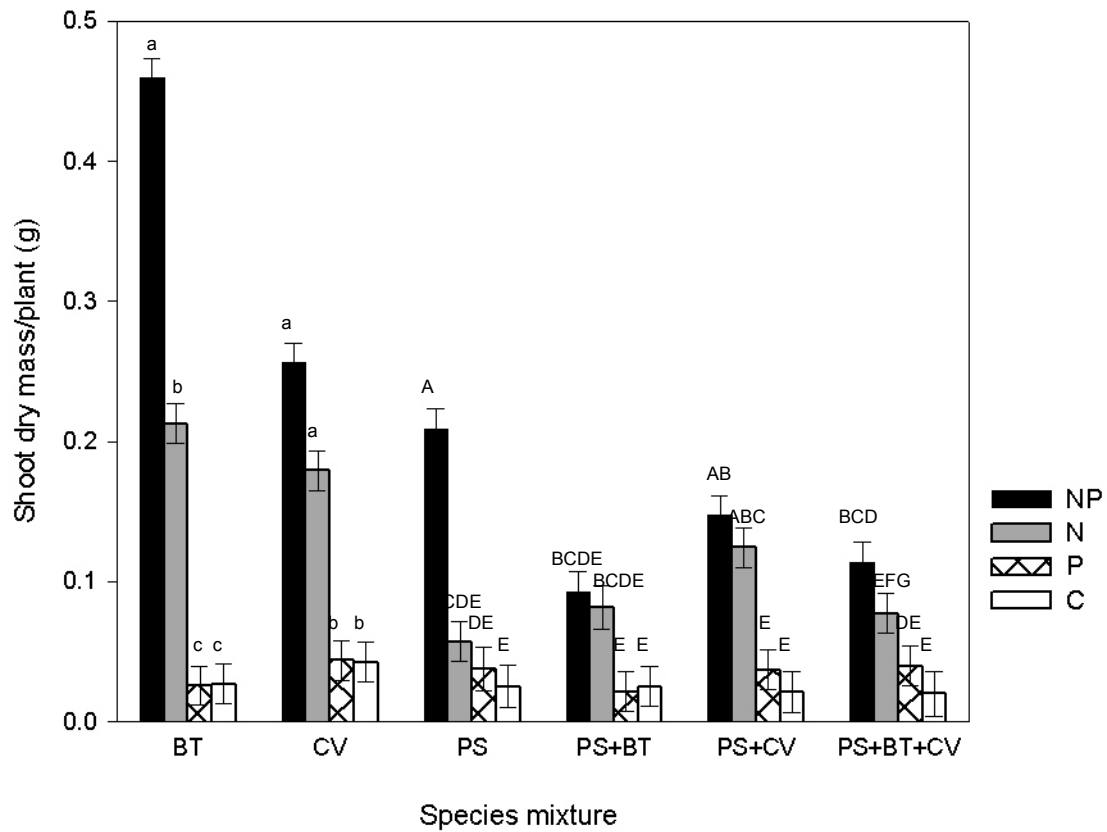


FIGURE 3.4. Relationship of mean (\pm SE) shoot dry mass to species mixture at harvest. Treatment codes are C, control; P, phosphorus added; N, nitrogen added; and NP, both nutrients added. Species mixture codes across the horizontal axis are BT, *Bromus tectorum* monoculture; CV, *Centaurea virgata* monoculture; PS, *Pseudoroegneria spicata* monoculture; PS+BT, *P. spicata* surrounded by *B. tectorum*; PS+CV, *P. spicata* surrounded by *C. virgata*; and PS+BT+CV, *P. spicata* surrounded by *B. tectorum* and *C. virgata*. Different lower case letters represent significant differences ($P \leq 0.05$) within a given invasive monoculture, and uppercase letters represent significant differences ($P \leq 0.05$) among all pots with a *P. spicata* target.

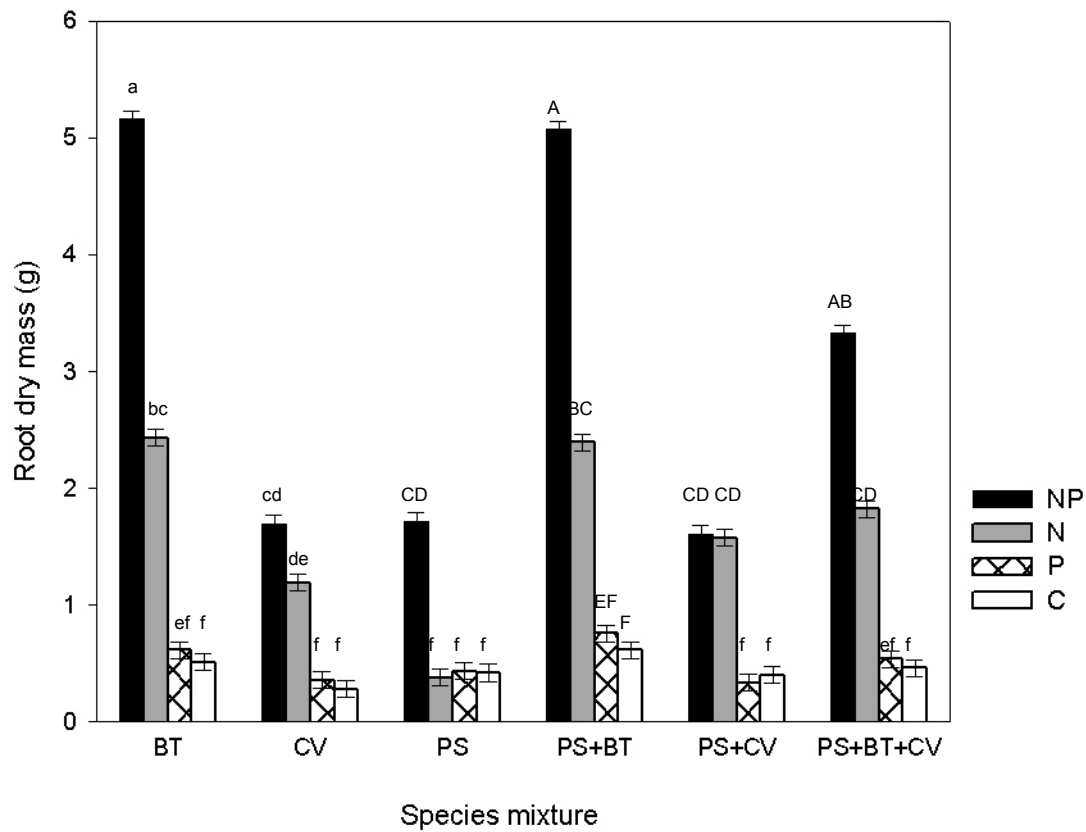


FIGURE 3.5. Relationship of mean (\pm SE) total pot root dry mass to species mixture at harvest. Treatment codes are C, control; P, phosphorus added; N, nitrogen added; and NP, both nutrients added. Species mixture codes across the horizontal axis are BT, *Bromus tectorum* monoculture; CV, *Centaurea virgata* monoculture; PS, *Pseudoroegneria spicata* monoculture; PS+BT, *P. spicata* surrounded by *B. tectorum*; PS+CV, *P. spicata* surrounded by *C. virgata*; and PS+BT+CV, *P. spicata* surrounded by *B. tectorum* and *C. virgata*. Different lower case letters represent significant differences ($P \leq 0.05$) within a given invasive monoculture, and uppercase letters represent significant differences ($P \leq 0.05$) among all pots with a *P. spicata* target.

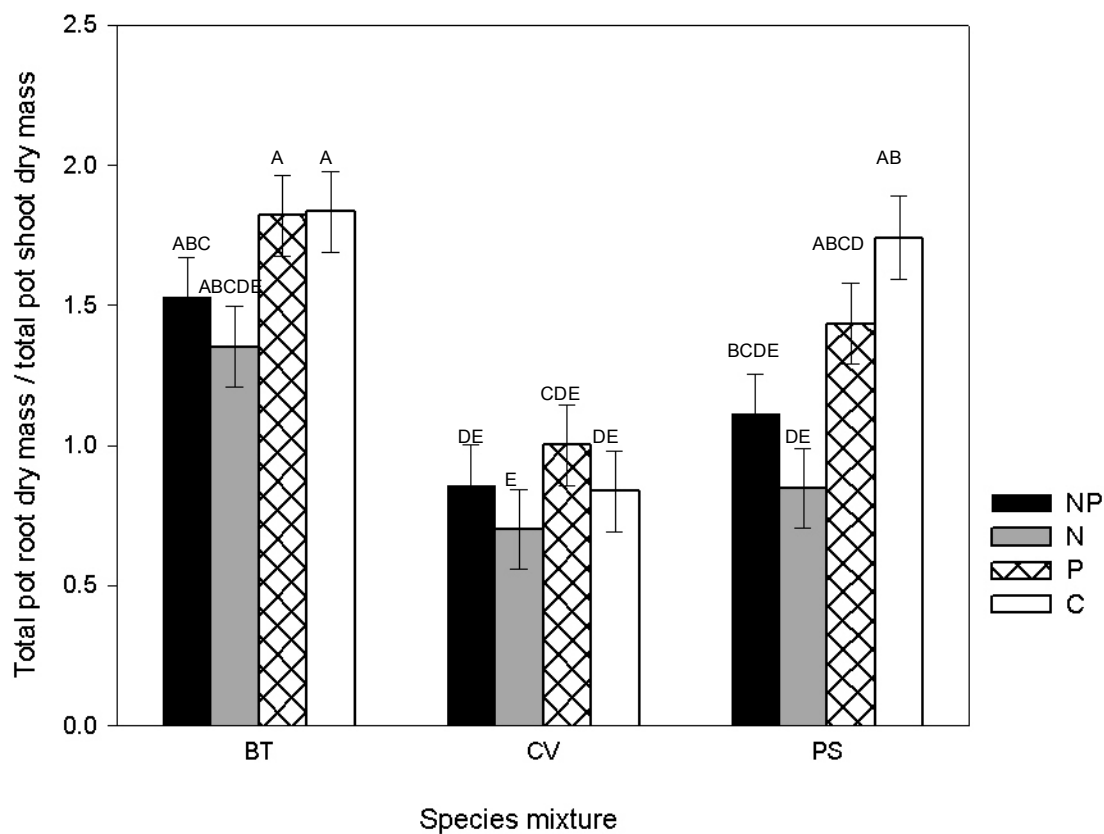


FIGURE 3.6. Relationship of mean (\pm SE) root dry mass/shoot dry mass to species mixture at harvest. Treatment codes are C, control; P, phosphorus added; N, nitrogen added; and NP, both nutrients added. Species mixture codes across the horizontal axis are BT, *Bromus tectorum* monoculture; CV, *Centaurea virgata* monoculture; and PS, *Pseudoroegneria spicata* monoculture. Different letters represent significant differences ($P \leq 0.05$) among pots.

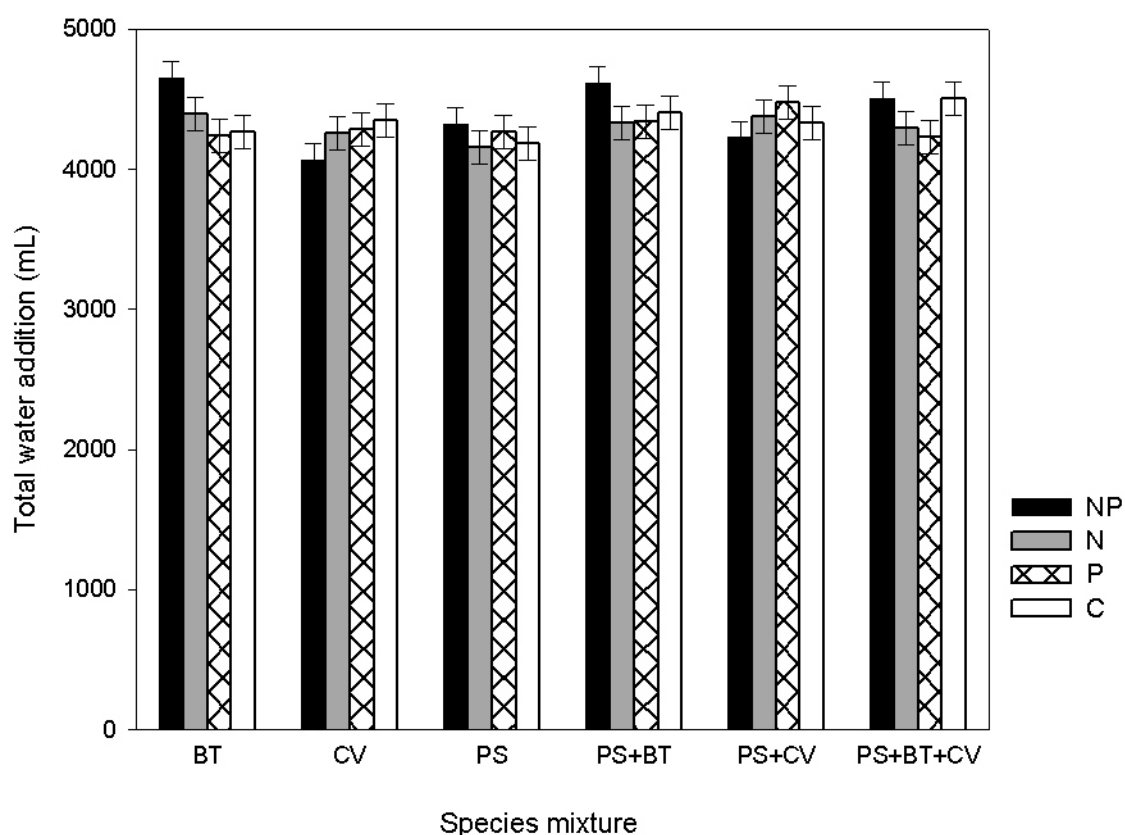


FIGURE 3.7. Relationship of mean (\pm SE) total water addition to species mixture at harvest. Treatment codes are C, control; P, phosphorus added; N, nitrogen added; and NP, both nutrients added. Species mixture codes across the horizontal axis are BT, *Bromus tectorum* monoculture; CV, *Centaurea virgata* monoculture; PS, *Pseudoroegneria spicata* monoculture; PS+BT, *P. spicata* surrounded by *B. tectorum*; PS+CV, *P. spicata* surrounded by *C. virgata*; and PS+BT+CV, *P. spicata* surrounded by *B. tectorum* and *C. virgata*.

CHAPTER 4

CONCLUSION

Exotic plant invasions of the Intermountain West result in large economic losses, degradation of ecological function, and a reduction in floristic diversity (D'Antonio and Vitousek 1992, Knapp 1996, Vazquez et al. 2008a). In particular, the annual exotic grass *Bromus tectorum* has altered fire regimes and displaced many valuable native perennial grasses such as *Pseudoroegneria spicata*. Two factors contribute to some of the low success rates of previous attempts to restore native perennial grasses to invaded rangelands: excessive resource competition from exotic populations during the establishment phase (Pyke and Borman 1993, Mazzola et al. 2008), and an insufficient understanding of the basic ecological mechanisms responsible for the competitive advantages of successful invaders (Sakai et al. 2001, Vazquez et al. 2008b, Krueger-Mangold et al. 2006). Competition theory suggests that many native species should possess a competitive advantage over early successional species, like *B. tectorum*, for scarce soil nutrients (Tilman 1988, Wedin and Tilman 1990). Recent work has resulted in restoration of perennial vegetation to invaded semi-arid rangelands by impoverishing the soil of N with labile C amendment (McLendon and Redente 1992, Paschke et al. 2000). More limited study indicates that P also limits semi-arid vegetation systems and can be immobilized with soil amendments (Redente et al. 1992, Craine et al. 2008), but little attention has been given to understanding how these two soil nutrients interact to affect plant growth.

I evaluated the results of soil nutrient impoverishment in a field setting in Chapter 2. Following addition of C in the form of sucrose, I applied N (ammonium nitrate) and P

(triple super phosphate) to a simple vegetation community comprising monocultures and mixtures of *P. spicata*, *B. tectorum*, and *Centaurea virgata*. *Centaurea virgata* is an exotic perennial forb that has invaded parts of the Great Basin, especially in Utah. Occasionally, suppression of *B. tectorum* opens a niche that other invasive weeds fill before native species are successfully established, and I determined that *C. virgata* produced as much or more biomass than the other two species. In terms of biomass in the field experiment, *C. virgata* increased with P addition, *B. tectorum* increased with N addition, and *P. spicata* increased with N addition and P addition. Soil N and P interacted to affect physiological activity of all species. Photosynthetic rate of *P. spicata* was greatest in unfertilized control plants in monoculture, whereas *C. virgata* photosynthesized most rapidly in control plants in competition with *P. spicata*. For *B. tectorum*, stomatal conductance and transpiration were also maximized in competition with *P. spicata* when treated with N and P together, or unfertilized. The same responses were minimized when unfertilized in competition with all three species.

In Chapter 3, I cultivated in the greenhouse simple communities with the same three species, but interspecific competitive effects were only assessed on *P. spicata*. I used a sandy soil that was very low in available N and P, and I supplied these nutrients in the form of ammonium nitrate and mono- and dibasic sodium phosphate. Tiller number, leaf number, specific leaf area, shoot dry mass, and root dry mass were recorded, and all species showed a strongly positive response to nutrient addition. *Pseudoroegneria spicata* had a smaller magnitude response than did *B. tectorum*, suggesting a smaller degree of limitation. *Pseudoroegneria spicata* was more efficient than the other species, but was outgrown considerably by *B. tectorum*. Growth of *P. spicata* increased

significantly only when receiving N and P together. *Bromus tectorum* also grew best with both nutrients added, but still experienced substantial increases with N alone; P alone had no effect. Early after treatment, *C. virgata* was co-limited by N and P, similar to *P. spicata*, but within two months, only N had increased its growth responses.

This research indicates soil N and P can each stimulate growth of annual and perennial grasses in the Great Basin, implying the possibility of joint limitation depending on soil conditions. Although low N conditions will often inhibit growth of the species I investigated, P immobilization could negate an additional competitive advantage of invasive species. *Centaurea virgata* may be either less sensitive to P than the grasses, or alternatively, a superior competitor for P. The similar performance I observed across life form and nativity status suggest that interference from invasive species is reduced at the low nutrient levels, making successful native establishment more likely. Confirmation of these results in a variety of field settings, however, is still needed.

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